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NEW GENERA AND SPECIES OF NORTH AMERICAN MIRIDAE (HEMIPTERA)

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The genus Anapus Stal is well known in the Palearctic region where nine species are recognized. The writer held the first specimen of an American species of Anapus for several years hoping more material might turn up for publication. The time has come when we wish to present this and a few other interesting species for the printed record.

Anapus americanus new species.

Allied to nigritus Jak. but differs in having the male brachypterous, clothed with silvery, scale-like vestiture intermixed with fine, short yellowish simple hairs; antennal segment III longer than segment II. Scale-like silvery hairs cover the front of head, sides and tergites of the abdomen, thorax, and pad-shaped hemelytra.

♂. Length 2.4 mm, width of abdomen 1.48 mm. Brachypterous, the hemelytra reduced to small pads that cover only the first four segments of the abdomen. Head: width .90 mm; vertex .22 mm; brownish black, a pallid spot just beneath the eye. Antennal segment I, length .45 mm, cylindrical (width .075 mm), dorsal surface of apical half bearing four or five erect, black bristles, color reddish black; II, length 1.24 mm, slender, cylindrical, clothed with short fine pubescence, reddish brown, darker apically; III, .72 mm, slightly more slender than II, brownish black; IV, .51 mm, brownish black. Rostrum, length .99 mm, reaching upon middle of hind coxae, reddish black, first segment very thick as characteristic for the genus. Pronotum: length .45 mm, width at base .72 mm, cylindrical as viewed from above, basal margin slightly sinuate, anterior angles rounded off slightly, surface of disk transversely rugulose, impunctate.

Hemelytra reduced to small pads, each about as long as wide, making contact for a short space behind apex of scutellum. Scutellum triangular, convex on middle but rounded off each side to basal angles which fit the sybcylindrical pronotum. Legs reddish brown, dorsal side of tibiae paler; tibia set with strong black bristles; hind femora strongly developed for jumping, dorsal margin set with a row of black bristles. Abdomen broadly ovate, genital segment strongly deflexed; connexivum sharply elevated, its inner edge narrowly pallid bordering the tergites.

Holotype: ♂ June 21, 1932, Tieton Canyon, Washington; (A.R. Rolfs); author's collection. Presumably the "Tieton Canyon" is a canyon on the Tieton River. Paratype: ♂ July 30, 1904, Logan, Utah. Recently, other specimens bearing the same label were received by Dr. L. A. Kelton from G.F. Knowlton of Logan, Utah. The figures of Anapus americanus were made by Dr. Kelton and forwarded to the author for identification. When informed of our manuscript on Anapus, Dr. Kelton kindly offered the same for inclusion in the present paper.

Ballella new genus

Arolia slender, erect, subparallel but converging at apices; genital segment, claspers and the legs are of the type found in Parthenicus, but distinguished at once by the thickened first and second antennal segments. The small size of the insect and the thickened antennal segments suggest that it might belong in the Phylinae, but the arolia and form of the genital segment show its true position to be in the Orthotylinae and related to the genus Parthenicus (Fig. 3). Head and antennae as shown in the figure; vertex broad, flattened, ecarinate, clypeus and sides of head glabrous, shining black; frons, vertex and ventral surface of head, pallid and clothed with sericeous, silky pubescence. Rostrum reaching upon base of abdomen, or to base of the ovipositor in the female. Both sexes with the first antennal segment very thick, nearly equal to diameter of segment II, in length extending somewhat beyond apex of the prominent clypeus (Fig. 2); length of segment II equal to three times the length of segment I, nearly equal in thickness but tapering to more slender on apical third; clothed with very fine, short, simple pubescence; segments III and IV very slender, combined length only equal to half the length of segment II.

Body bearing two types of pubescence, sparsely clothed with simple, suberect hairs, and intermixed with recumbent, sericeous silky pubescence as found in Parthenicus. Legs as in Parthenicus, with hind femora thickened, long and tapering, adapted for jumping; tibiae rather long, bearing spines which in length about equal diameter of tibia.

In the keys of Carvalho (1955), Ballella runs to Excentricus Reuter from which it may be separated by the longer second antennal segment which is three times the length of segment I; also distinguished by the thick first antennal segment which in length does not equal width of vertex; head more flattened and the vertex relatively broader; clypeus and sides of head glabrous, polished, shining black.

Type of genus: Ballella basicornis new species.

Ballella basicornis new species.

Distinguished by the small size and the greatly thickened first and second antennal segments; general coloration pallid, antennae black, the clypeus, sides of head and eyes shining black.

Male. Length 2.3 mm. Head: width .58 mm, vertex .30 mm; pallid, clypeus, sides of head and eyes shining black, suggesting the wearing of a black mask. Rostrum, length .92 mm, reaching upon base of abdomen, pallid, apical half fuscous. Antennae: segment I, length .23 mm, width at apex .14 mm, black, having three short bristles on inner face; II, .72 mm, width .15 mm, tapering to more slender on apical one-third, uniformly black, clothed with very fine, recumbent, simple dusky pubescence; III, .24 mm, slender, fuscous on apical half; IV, .20 mm, pallid, apical half fuscous. Pronotum: length .36 mm, width at base .78 mm, disk only moderately convex, lateral margins slightly concave; disk, scutellum, as well as surface of head and wings, sparsely clothed with suberect simple pubescence and intermixed with more closely appressed, scalelike silvery hairs; color pale cream, anterior angles of disk and basal line of calli, fuscous, pleura with black spot beneath anterior angles and covering the coxal cleft. Scutellum triangular, only slightly convex.

Hemelytra pallid to cream, half of clavus and corium shaded with fuscous, apical edge pale. Cuneus fuscous, outer edge and apex pale. Membrane dusky, a fuscous spot behind apex of cuneus. Legs suggestive of the form and colors seen in species of Parthenicus; hind femora extending for half their length beyond tip of abdomen, pallid, anterior aspect with three rows of reddish brown spots, obsolete on basal one-third and obscured with fuscous and brown on the apical one-third, front and middle femora more pallid, with reddish brown spots much reduced. Tibiae pallid, hind pair ornamented with six red brown spots, only three or four on the front and middle tibiae; set with two rows of fine spines. Abdomen rather short, genital segment concave apically, claspers rather small but distinctive (Fig. 3).

Female. Length 2.4 mm, width 1.0 mm. Head: width .61 mm, vertex .32 mm. Antennae: segment I, length .24 mm, width at apex .16 mm; II, length .82 mm, width .18 mm, tapering to more slender on apical third; III, .27 mm, slender, .04 mm,thick; IV, .26 mm, slender; pubescence and color similar to the male. Rostrum, length 1.25 mm, reaching beyond hind coxae to base of the ovipositor. More robust than the male, but very similar in color and pubescence.

Holotype: ♂ May 5, 1931, Phoenix, Arizona (E. D. Ball, collector); author's collection. Allotype: same data as the type. Paratypes: 22♂♀, taken with the types on a "white mat-like plant," growing flat on the ground like a spurge (Euphorbia). The plant was not identified as to genus by Dr. Ball. For a number of years Dr. Ball sent to the author the miscellaneous Miridae which he collected, and in return we sent to him collections of Cicadellidae and Membracidae. The genus is named in honor of Dr. E. D. Ball, an outstanding authority on Cicadellidae and Membracidae.

Beamerella new genus

Allied to Hambletoniola Carv., but differs in having both second and third antennal segments strongly inflated; the first, second and third antennal segments sparsely set with large, black, flat scalelike bristles which stand erect (Fig. 1). In Hambletoniola only the third antennal segment is inflated, the second antennal segment cylindrical and clothed with erect, silvery, scalelike hairs. Both genera belong in the Phylinae as the genital segment, claws and pseudarolia are very similar to those found in Psallus and Plagiognathus.

Head broad, vertex very wide, more than three times the dorsal width of an eye. Body clothed with two types of pubescence, simple, suberect hairs intermixed with more recumbent, sericeous, silky pubescence; body surface and legs sprinkled with fuscous dots from which arise simple fuscous hairs.

Type of genus: Beamerella personatus new species.

Beamerella personatus new species.

A small robust species of pallid color, sprinkled with small fuscous dots; antennae black, second and third segments strongly inflated; head with clypeus and sides of head shining black, giving the appearance of wearing a black mask.

Male. Length 2.6 mm, width 1.36 mm. Head: width .88 mm, vertex .56 mm; clypeus scarcely visible from above, shining black, vertex and basal area of frons pallid, eyes brownish; the black color suggesting a mask. Rostrum, length 1.2 mm, extending beyond hind coxae to second ventral segment, pale, apical segment black. Antennae: segment I, length .20 mm, width at apex .10 mm, black; II, .48 mm, width .20 mm at middle, tapering smaller at base and apex, shining black, set with several large, erect, black scalelike bristles which are also found on the first and third segments; III, .38 mm, width .17 mm, tapering to more slender on apex, black; IV, .30 mm, width .10 mm, tapering more slender on apical half, brownish black, apical half pallid. Pronotum: length .47 mm, width at base 1.05 mm, disk slightly convex, lateral margins nearly straight. Body including the hemelytra uniformly pallid, above and below sparsely set with tiny fuscous dots from which the larger pubescent hairs arise; clothed with two types of pubescence, simple, suberect pubescent hairs, intermixed with recumbent, sericeous, silvery pubescence. Membrane milky white, springled with fuscous dots, a rounded black spot each side on the margin beyond apex of cuneus. Legs pale to yellowish, femora dotted with fuscous, one large black dot at middle of ventral surface; tibial spines yellowish, each spine arising from a black dot, spines prominent, their length greater than diameter of tibia. Genital segment very similar to that found in Psallus, the black bladelike tip of the spiculum turned to the left side and resting across middle of left clasper. Right clasper small, triangular in form, apex ending in a tiny hook.

Female. Length 2.6 mm, width 1.3 mm. Head: width .85 mm, vertex .54 mm. Antennae: segment I, length .20 mm, width .10 mm; II, .42 mm, width at middle .18 mm, tapering smaller at base and apex, set with erect, black scalelike bristles as in the male; III, .30 mm, width .15 mm, tapering more slender on apical half; IV, .28 mm, width .10 mm, brownish black, apical half pallid; first three segments shining black and set with black scalelike bristles as found in the male. Rostrum, length 1.12 mm, reaching upon second ventral segment. Very similar to the male in pubescence and coloration.

Holotype: ♂ July 9, 1939, Marathon, Texas (R.H. Beamer); University of Kansas, Snow collection. Allotype: same data as the type. Paratypes: 12♂♀, taken with the types: 1♂ 3♀, July 10, 1938, 65 miles south of Marathon, Texas (R.H. Beamer); Kansas University Collection, also specimens in author's collection and Iowa State College collection. The genus is named in honor of Dr. R. H. Beamer, who was well known for his work on family Cicadellidae.

Chlamydatus ruficornis new species.

Allied to evanescens Boh. but differs in relative lengths of antennal segments; length of segment II subequal to combined lengths of segments III and IV; antennal segments I and II uniformly reddish while segments III and IV are brownish black. General color black, with antennae, rostrum and tibiae reddish.

Male. Length 1.9 mm, width .85 mm. Head: width .75 mm, vertex .34 mm; clypeus visible from above, smoothly confluent with frons. Rostrum, length .99 mm, reaching to middle of hind coxae, reddish.

Antennae: segment I, length .32 mm, thickness .08 mm, reddish, dusky on base, with two black bristles dorsally on apical half; segment II, .67 mm, thickness .08 mm, uniformly reddish, clothed with short, recumbent, pallid pubescence; III, .34 mm, brownish black; IV, .33 mm, black. Pronotum: length .40 mm, width at base .65 mm, anterior width only slightly less; basal margin slightly sinuate, disk moderately convex, sloping gradually to anterior and lateral margins, surface here as elsewhere showing a dull waxlike finish. Dorsum, body and legs clothed with short, recumbent, pallid to yellowish simple pubescence. Hemelytra short, covering about half of the abdomen, membrane absent. Legs built for leaping, hind femora thick and broad, femora and coxae blackish brown, apices more reddish; tibiae dull reddish, spines black, without spots at base, tarsi fuscous brown.

Female. Length 2.30 mm, width of abdomen 1.20 mm. Head: width .77 mm, interocular width .35 mm. Antennae: segment I, length .30 mm, width .08 mm; II, .64 mm, width on apical half .096 mm, tapering to more slender on basal half, apex infuscated; III, .32 mm, black; IV, .32 mm, black. More robust than the male but very similar in the abbreviated hemelytra, coloration and pubescence.

Holotype: ♂ July 22, 1940, Ames, Iowa (H.H. Knight), author's collection. Allotype: same data as the type. Paratypes: 22♂, 18♀, taken with the types, in low lying pasture on the edge of Squaw creek valley, about two miles northwest of Ames. The pasture was grazed fairly short by cattle. The bugs were found among short clover plants and none were taken by sweeping taller grass and weeds. Also 1♂ 2♀ July 21, 1940, Ames, Iowa (H. M. Harris) taken in the same pasture. COLORADO: ♀ April 30, ♂♀ May 13, 1898 "N. Colo." (E.D. Ball).

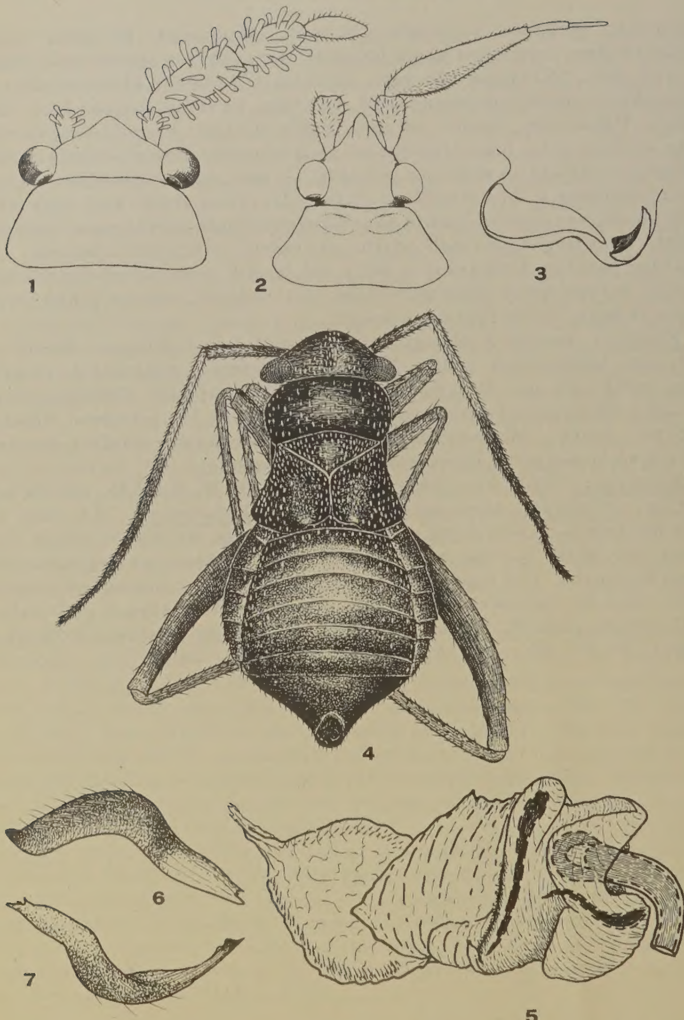

Fig. 1. Beamerella personatus, new genus, new species.
Fig. 2. Ballella basicornis, n. gen., n. sp.
Fig. 3. Ballella basicornis, male claspers, posterior aspect.
Fig. 4. Anapus americanus, n. sp., male.
Fig. 5. Anapus americanus, vesica, ventral aspect.
Fig. 6. Anapus americanus, right clasper, ventral aspect.
Fig. 7. Anapus americanus, left clasper, posterior aspect.

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CORRECTION OF THE OBSERVED RATIO FOR ERRORS ASSOCIATED WITH ION CURRENT COLLECTION AND AMPLIFICATION IN DUAL COLLECTOR MASS SPECTROMETERS

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Because of isotopes, the mass spectra of most elements and the spectra of nearly all compounds contain more than one mass peak for each species of ions. These peaks are usually separated by one mass unit as in $^{28}N_2^+$, $^{29}N_2^+$, and $^{30}N_2^+$; or are separated by two mass units as in $^{36}A^+$, $^{38}A^+$, and $^{40}A^+$. Frequently dual collector mass spectrometers are employed to determine the ratio of two ion currents due to these isotopes. In these instruments a null method (2) is generally used to determine the ion current ratios. This involves amplifying the two currents with separate amplifiers and then comparing the amplified currents by means of some type of balancing bridge network (3). Thus a value for the ratio is obtained as a resistance measurement on a decade voltage divider.

To obtain the true isotopic ratio of a sample gas, it is necessary to separately correct the observed ratio obtained from the mass spectrometer for each source of error. While this cannot be completely achieved in practice, it can be closely approached. Common sources of error inherent in most mass spectrometers are listed below:

A. Gas flow from the manifold to the source.
B. Gass flow from the source.
C. Residual gas in the system.
D. Gas adsorbed on the surfaces in the instrument.
E. Gas absorbed in the components in the instrument.
F. Differences in ionization efficiencies of the isotopes.
G. Secondary reactions occurring in the source.
H. Charge change between particles in sector instruments.
I. Overlap of the ion beam onto the No. 1 collector.
J. Difference in amplification characteristics of the two amplifier circuits.

These errors can be divided into those that occur before the ions leave the source (A-G), and those that arise after the ions have left the source (H-J). The following discussion will deal only with those errors associated with the collection and amplification of ion currents in the mass tube. In many dual collector instruments, a slit in the first collector plate makes it possible for an ion beam to pass through the slit to a second collector plate positioned behind the first (4). The amplified currents from these two collectors are used to obtain the ratio.

The potential errors (I, J) listed above are introduced into ratio determinations with this arrangement. One is caused by part of the ion beam, which is focused on the No. 2 collector, falling on the No. 1 collector and the other is due to the fact that both amplifier channels may not be identical. If the ion beam focused on the No. 2 collector is wider than the slit in the No. 1 collector, part of the ion beam will fall on the No. 1 collector and be included in the ion current collected by it. This will be called overlap in this presentation and the amount falling on the No. 1 collector is expressed as a percentage of the total ion beam (ion current on No. 2 collector plus overlap). The effect of overlap is an observed ratio lower than the true ratio. If there are differences in the amplifier channels, the effect on the ratio will depend upon which channel has the higher over-all factor of amplification. A method has been developed whereby the true ratio of two currents reaching the dual collectors may be determined from the observed ratio obtained by the null method (2).

The method consists of two parts. The first part is the computation of the percent overlap and ratio of the amplification factors. The second part is the application of these correction factors to the ratio of the ion current simultaneously reaching the No. 2 collector to that reaching the No. 1 collector.

The first part involves observing the magnitude of a single mass peak separately on each collector. The procedure is as follows: Introduce into the mass spectrometer a gas whose spectrum will contain one major mass peak with no other peaks within two or preferably three mass units of it. This gas can be high purity argon, high purity nitrogen 14, or any other suitable gas.[1] Focus the ion beam on the No. 2 collector and read the output from the No. 1 and No, 2 amplifiers by using a battery across the decade voltage divider of the balancing network and achieving a null point for each amplifier. Then move the peak so that it falls only on the No. 1 collector and again read the amplifier output versus the battery on the decade divider. These three readings should be obtained as precisely as possible and should be obtained at more than one pressure. The three readings at any one pressure will be used to calculate the correction factors. These can then be checked for consistency by comparison with those calculated at different pressures.

The following notation will be used in the calculations:

C_{12} = Ion current from No. 1 amplifier with peak focused on No. 2 collector.

C_2 = Ion current from No. 2 amplifier with peak focused on No. 2 collector.

C_1 = Ion current from No. 1 amplifier with peak on No. 1 collector only. (All ion currents expressed as decade units.)

L = Percentage overlap onto No. 1 collector.

β_1 = Over-all amplification of No. 1 amplifier.

[1]A limited supply of 99.95+ atom percent N^{14} in the form of recrystallized $[NH_4]_2SO_4$ can be obtained for a nominal service charge from the Ames Laboratory of the U.S. Atomic Energy Commission, Ames, Iowa. Address all inquiries in care of the Director of the Laboratory.

β_2 = Over-all amplification of No. 2 amplifier.
K = β_1/β_2. (In inverse feedback amplifiers this will be very close to the ratio of the input resistor values.)

The correction factors (L and K) are obtained as shown below:
The ratio K of β_1/β_2 can be found by this equation,

$$K = \beta_1/\beta_2 = \frac{C_1 - C_{12}}{C_2} \tag{1}$$

The percentage overlap (L) can then be found by this equation,

$$L = \frac{\frac{C_{12}}{K}}{C_2 + \frac{C_{12}}{K}} \times 100 \tag{2}$$

or

$$L = \frac{C_{12}}{KC_2 + C_{12}} \times 100 \tag{3}$$

The calculation of K and L is illustrated by a sample calculation. Assume the following observed ion currents as indicated by the amplifier outputs:

C_{12} = 22 decade units
C_2 = 980 decade units
C_1 = 1100 decade units.

From equation (1) K is calculated as:

$$K = \frac{C_1 - C_{12}}{C_2} = \frac{1100 - 22}{980} = 1.100 .$$

From equation (3) L is calculated as:

$$L = \frac{C_{12}}{KC_2 + C_{12}} \times 100 = \frac{22}{(1.1)(980) + 22} \times 100 = 2.00 .$$

The second part involves the ratio of two ion currents simultaneously reaching the collector. The notation used in speaking of different ratios is as follows:

R_0 = Observed ratio of the ion current on No. 2 collector to that on the No. 1 collector.
R_K = Observed ratio corrected for amplifier differences.
R_T = True ratio of ion current No. 2 to ion current No. 1.

To obtain R_T (true ratio of ion currents reaching the collector end), the observed ratio obtained directly from the instrument should first be corrected for the difference in amplification; i.e., the factor K is applied.

$$R_K = KR_0 \tag{4}$$

The correction for overlap can then be applied to find the true ratio of the ion currents reaching the collectors.

$$R_T = \frac{R_K + \dfrac{L}{100 - L} R_K}{1 - \dfrac{L}{100 - L} R_K} \tag{5}$$

or

$$R_T = \frac{100\ R_K}{100 - L(1 + R_K)} \tag{6}$$

By combining equations (4) and (6) the true ratio can found from the observed ratio by the following equation.

$$R_T = \frac{100\ KR_0}{100 - L(1 + KR_0)} \tag{7}$$

Equation (7) can be applied to any ratio which can be read on the instrument. It gives the absolute ratio of the currents reaching the collector end. It does not correct isotope abundance ratios for gas flow, background, adsorbed gases, ionization efficiency differences or secondary source reactions. A means of calibrating mass spectrometers for some of these errors has been previously presented (1).

The authors wish to acknowledge the helpful discussions concerning this research with Gregor Junk, Gerald Flesch, Arthur Anderson, and H. Gene Staley.

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IOWA STATE COLLEGE JOURNAL OF SCIENCE
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A METHOD OF APPLYING EXTREMAL METHODS TO PROBLEMS OF ELECTRICAL RESISTANCE*

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INTRODUCTION

In a paper by Carlson and Hendrickson[1] use has been made of variational methods to secure upper and lower limits for electrical resistance. These methods, as presented, were based on techniques formulated by Schwinger and involved consideration of an integral equation for the current- or potential-distribution at a boundary surface. The presentation of Carlson and Hendrickson has the advantage of suggesting the applicability of similar techniques to problems in other fields of physics but, for this reason, may suffer from a lack of obvious physical motivation for the detailed mathematical steps. It is the purpose of the present note to indicate that the same technique may be introduced for resistance problems, in what may appear to be a more natural way, by use of well-known extremal theorems for resistance. It may be supposed that analogous extremal theorems exist in other fields of physics and that in some cases direct application of these theorems will lead to useful alternative methods of solution for specific problems.

B. UPPER LIMIT TO RESISTANCE

Use is made of the theorem[2] that an upper-limit, $R_{u.\ell.}$, is given by

$$R_{u.\ell.} \equiv \frac{\iiint \rho J^2 \, d\tau}{\left[\iint \vec{J} \cdot \vec{ds}\right]^2},$$

where ρ is the resistivity of the material and $\vec{J}$ is an assumed current distribution (for which div $\vec{J} = 0$) such that $\rho \vec{J}$ is not necessarily derivable

* Contribution No. 668.

[1] J.F. Carlson and T.J. Hendrickson. 1953. Variational methods for problems in resistance. Ames Laboratory Manuscript LR-132: Jour. Appl. Physics 24:1462-1465.

[2] Cf. W.R. Smythe. Static and Dynamic Electricity (McGraw-Hill Book Company, Inc., New York, 1950) second edition, sect. 6.11, p. 233; or see Appendix I. This theorem is analogous to Thomson's theorem in electrostatics.

from a potential or, if it is, the potential from which it may be derived is not necessarily constant over the electrodes.

In terms of any assumed emergent current distribution, J_n, at one of the electrodes (designated as electrode number two), it is appropriate to consider the current distribution throughout the resistive medium to be

$$\vec{J} = \frac{1}{\rho}\,\mathrm{grad} \iint_2 \mathcal{G}_1\, J_n\, ds\ ,$$

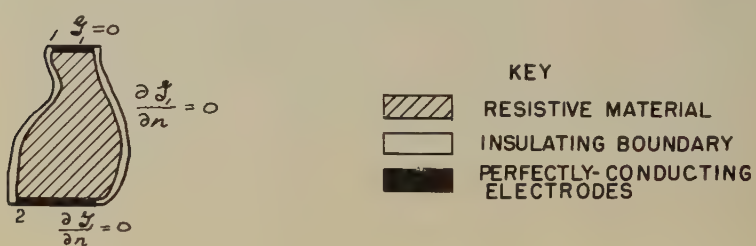
where $\mathcal{G}_1$ is a Green's function, of $\vec{r}$ and $\vec{r}'$, such that

(i) $\mathrm{div}(\frac{1}{\rho}\ \mathrm{grad}\, \mathcal{G}_1) = -\ \delta(\vec{r}-\vec{r}\,'),$

(ii) $\mathcal{G}_1 = 0$ on electrode number 1, and

(iii) $\frac{\partial \mathcal{G}_1}{\partial\ n} = 0$ on the other boundaries of the resistive material.

$\mathcal{G}_1$ thus represents the potential arising from a point source of unit current when electrode number one serves as the sink.



It will be noted that the expression considered for $\vec{J}$ is such that, if J_n were the true distribution of the emergent current, the expression $-\iint_2 \mathcal{G}_1\, J_n\, ds$ would represent the true potential function for the problem, save for an arbitrary constant term. That this is so is seen from the use of Green's theorem (equivalent to a reciprocation theorem for currents):

$$V = -\iint \frac{V\partial\, \mathcal{G}_1/\partial\, n}{\rho}\, ds + \iint \frac{\mathcal{G}_1\, \partial\, V/\partial\, n}{\rho}\, ds$$

$$= V_1 - \iint_2 \mathcal{G}_1\, J_n\, ds\ .$$

By the nature of $\mathcal{G}_1$ as a source-function, the expression considered for $\vec{J}$ will, of course, be consistent with the J_n assumed at the electrode.

Accordingly

$$R_{u.\ell.} = \frac{\iiint (\vec{J} \cdot \operatorname{grad} \iint_2 \mathcal{G}_1 \, J_n \, ds) \, d\tau}{\left[\iint J_n \, ds \right]^2}$$

$$= \frac{\iiint \operatorname{div} (\vec{J} \iint_2 \mathcal{G}_1 \, J_n \, ds) \, d\tau}{\left[\iint J_n \, ds \right]^2} \quad \text{(since div } \vec{J} = 0 \text{ throughout the volume)}$$

$$= \frac{\iint ds' \iint J_{n'} \, \mathcal{G}_1 (\vec{r}', \vec{r}) \, J_n \, ds}{\left[\iint J_n \, ds \right]^2} ,$$

the integration being only over the surface of electrode number 2, since either J_n or $\mathcal{G}_1$ will vanish on the other boundaries of the medium. To obtain an estimate for the resistance one assumes a functional form for the emergent current distribution, J_n, which is presumed not to depart violently from the correct distribution and which is sufficiently simple to permit performing the indicated integrations without undue difficulty. Since the expression for $R_{u.\ell.}$ is homogeneous of degree zero in J_n, no further normalization is required.

By way of comparison with the example of Carlson and Hendrickson[1], it is noted that

$$G_1 = \frac{1}{2\pi\rho} \int_2 \mathcal{G}_1 \, d\phi ,$$

$$K_1 = \left[\frac{\pi b^2}{\ell} G_1 - 1 \right] \text{ at } z = \ell \qquad \text{(i.e., at electrode number 2), and}$$

$$\chi (r) \propto J_n(r) .$$

Hence, for that case,

$$R_{u.\ell.} = \rho \frac{\iint \chi (r') \, r' \, G_1(r', r) \, r \, \chi (r) \, dr' \, dr}{\left[\int \chi (r) \, r \, dr \right]^2}$$

$$= \frac{\rho \ell}{\pi b^2} \frac{\iint r \, \chi (r) \, [K_1(r, r') + 1] \, r' \, \chi (r') \, dr \, dr'}{\left[\int \chi (r) \, r \, dr \right]^2}$$

$$= \frac{\rho \ell}{\pi b^2} [1 + \Gamma] ,$$ in agreement with eq. (22) of the paper cited (LR-132).

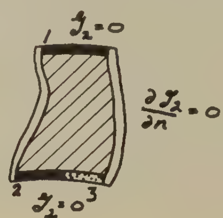
C. LOWER LIMIT TO RESISTANCE

In analogy with the procedure of section B, use is made of the theorem[3] that a lower limit, $R_{\ell.\ell.}$, is given by

$$\frac{1}{R_{\ell.\ell.}} \doteq \frac{\iiint \frac{1}{\rho} \, (\mathrm{grad}\ V)^2 \, d\tau}{V_o^{\,2}} ,$$

where V is a scalar function of position which assumes the specified values for the potential on the two electrodes and V_o represents the potential difference between the electrodes.

It is desirable to consider in this case, in addition to electrodes 1 and 2, a third surface, number 3, which physically forms a natural extension of electrode 2 but which constitutes an insulating boundary in the resistance problem of interest.



The potentials of electrodes 1 and 2 are then taken to be V_o and zero, respectively; the actual potential distribution over surface 3 is not known, but will be considered to be given by an assumed trial function, Φ .

Following again the procedure of Carlson and Hendrickson[1], use is made of a Green's function, $\mathcal{G}_2$, such that

(i) $\mathrm{div}\,(\frac{1}{\rho}\ \mathrm{grad}\, \mathcal{G}_2) = -\,\delta\,(\vec{r} - \vec{r}')$;

(ii) $\mathcal{G}_2 = 0$ on surfaces 1, 2, and 3; and

(iii) $\partial \mathcal{G}_2/\partial n = 0$ on the other boundaries of the resistive medium.

$\mathcal{G}_2$ thus represents the potential arising from a point source of unit current when surfaces 1, 2, and 3 serve as sinks at potential zero.

For use in the expression for $R_{\ell.\ell.}$ a potential distribution $V = V_1 + V_2$ is employed, where

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[3] See Appendix II; an essentially similar result in electrostatics is presented by H. Bateman, "Partial Differential Equations of Mathematical Physics" (Dover Publications, New York, 1944), sect. 2.41, p. 152.

$$V_1 = -V_0 \iint_1 \frac{1}{\rho} \partial \mathcal{G}_2/\partial n \; ds$$

and $$V_2 = -\iint_3 \frac{\Phi}{\rho} \frac{\partial \mathcal{G}_2}{\partial n} \, ds \; .$$

It is noted by use of Green's theorem or by the reciprocation theorem for currents, that V_1 represents the potential distribution which would be obtained if electrode 1 were at potential V_0, surfaces 2 and 3 at zero potential, and the remaining surfaces remained current barriers; similarly V_2 is the potential corresponding to a distribution Φ over surface 3, with electrodes 1 and 2 grounded and with the remaining surfaces impervious. The composite potential distribution V would be, in fact, the correct potential function for the problem at hand if the actual potential distribution over surface 3 were substituted for Φ .

By making use of the form adopted for V ,

$$\frac{1}{R_{\ell.\ell.}} = \frac{\iiint \frac{(\nabla V_1 + \nabla V_2)^2 \, d\tau}{\rho}}{V_0^{\,2}}$$

$$= \frac{\iiint \frac{1}{\rho} (\nabla V_1)^2 \, d\tau + 2 \iiint \frac{1}{\rho} \nabla V_1 \cdot \nabla V_2 \, d\tau + \iiint \frac{1}{\rho} (\nabla V_2)^2 \, d\tau}{V_0^{\,2}}$$

$$= \frac{1}{V_0} \iint_1 \frac{1}{\rho} \frac{\partial V_1}{\partial n} \, ds + \frac{1}{V_0^{\,2}} \iint_1 \frac{V_1}{\rho} \frac{\partial V_2}{\partial n} \, ds + \frac{1}{V_0^{\,2}} \iint_3 \frac{V_2}{\rho} \frac{\partial V_1}{\partial n} \, ds$$

$$+ \frac{1}{V_0^{\,2}} \iint_3 \frac{V_2}{\rho} \frac{\partial V_2}{\partial n} \, ds$$

$$= \frac{1}{R_0} - \frac{2}{V_0} \iint_3 \iint_1 \frac{\Phi}{\rho\rho'} \frac{\partial^2 V_2}{\partial n \partial n'} \, ds \, ds'$$

$$- \frac{1}{V_0^{\,2}} \iint_3 \iint_3 \frac{\Phi}{\rho} \frac{\partial^2 \mathcal{G}_2}{\partial n \partial n'} \frac{\Phi'}{\rho'} \, ds \, ds' \, ,$$

where R_0 is the resistance obtained when electrode 1 is at the potential V_0 and both surfaces 2 and 3 are grounded.

It is convenient to introduce the relative distribution of potential on surface 3:

$$\Psi \equiv \Phi / V_0 \, ,$$

whereupon

$$\frac{1}{R_{\ell.\ell.}} = \frac{1}{R_o} - 2\iint\limits_3\iint\limits_1 \frac{\Psi}{\rho\rho'}\frac{\partial^2 \mathcal{G}_2}{\partial n\,\partial n'}\,ds\,ds' - \iint\limits_3\iint\limits_3 \frac{\Psi}{\rho}\frac{\partial^2 \mathcal{G}_2}{\partial n\,\partial n'}\frac{\Psi'}{\rho'}\,ds\,ds'.$$

This last expression gives an upper limit to the conductance, and hence a lower limit to the resistance, in the problem of interest, through the use of various trial distributions for the potential on surface 3. In the form written it suffers, however, from the disadvantage that not only should a reasonable choice be made for the form of the trial potential, but also the scaling factor is of importance. For a given trial function, χ, a scaling factor f may be introduced such that $\Psi = f\chi$ and the last two terms in the expression for $\frac{1}{R_{\ell.\ell.}}$ become

$$-\,2f\iint\limits_3\iint\limits_1 \frac{\chi}{\rho\rho'}\frac{\partial^2 \mathcal{G}_2}{\partial n\,\partial n'}\,ds\,ds' - f^2\iint\limits_3\iint\limits_3 \frac{\chi}{\rho}\frac{\partial^2 \mathcal{G}_2}{\partial n\,\partial n'}\frac{\chi'}{\rho'}\,ds\,ds'.$$

The optimum choice of f, for a given χ, is

$$f = -\frac{\iint\limits_3\iint\limits_1 \frac{\chi}{\rho\rho'}\frac{\partial^2 \mathcal{G}_2}{\partial n\,\partial n'}\,ds\,ds'}{\iint\limits_3\iint\limits_3 \frac{\chi}{\rho}\frac{\partial^2 \mathcal{G}_2}{\partial n\,\partial n'}\frac{\chi'}{\rho'}\,ds\,ds'}$$

and the expression for $\frac{1}{R_{\ell.\ell.}}$ assumes the convenient homogeneous form:

$$\frac{1}{R_{\ell.\ell.}} \doteq \frac{1}{R_o} + \frac{\left[\iint\limits_3\iint\limits_1 \frac{\chi}{\rho\rho'}\frac{\partial^2 \mathcal{G}_2}{\partial n\,\partial n'}\,ds\,ds'\right]^2}{\iint\limits_3\iint\limits_3 \frac{\chi}{\rho}\frac{\partial^2 \mathcal{G}_2}{\partial n\,\partial n'}\frac{\chi'}{\rho'}\,ds\,ds'}.$$

The physical significance of the choice of scale factor may be seen in the following manner: For the correct distribution of voltage over surface 3, the current density, $J_n = -(1/\rho)(\partial V/\partial n)$, will be zero at each point on surface 3; thus

$$\frac{1}{\rho}\iint\limits_1 \frac{1}{\rho'}(\partial^2 \mathcal{G}_2/\partial n\partial n')\,ds' + \frac{1}{\rho}\iint\limits_3 \frac{\Psi'}{\rho'}(\partial^2 \mathcal{G}_2/\partial n\partial n')\,ds'$$

will then be zero at each point of surface 3. In the present case the trial function χ has been scaled in such a way that the integral $\iint\limits_3 \Psi J_n\,ds$ vanishes; i.e., so that

$$\iint\limits_3\iint\limits_1 \frac{\Psi}{\rho\rho'}\frac{\partial^2 \mathcal{G}_2}{\partial n\partial n'}\,ds\,ds' + \iint\limits_3\iint\limits_3 \frac{\Psi}{\rho}\frac{\partial^2 \mathcal{G}_2}{\partial n\partial n'}\frac{\Psi'}{\rho'}\,ds\,ds' = 0\ .$$

This condition imposed on Ψ then clearly includes the case in which Ψ assumes the true values of Φ/V_o.

A simplification results in the special case that $\frac{1}{V_o}\frac{\partial V_1}{\partial n}$ is independent of position on surface 3 and (say) equals $-1/L$. This situation arises, for example, in a problem in which V_1 represents the potential in a conductor of constant cross-section and of constant resistivity across the cross-section, as in the example of reference 1. In this case the double surface integral which appears in the numerator above, and which is identical with

$$-\frac{1}{V_o}\iint_3 \frac{\chi}{\rho}\frac{\partial V_1}{\partial n}\,ds, \text{ becomes } \frac{1}{L}\iint_3 \frac{\chi}{\rho}\,ds \text{ and we obtain}$$

$$\frac{1}{R_{\ell.\ell.}} = \frac{1}{R_o} + \frac{1}{L^2}\;\frac{\left[\iint_3 \frac{\chi}{\rho}\,ds\right]^2}{\iint_3\iint_3 \frac{\chi}{\rho}\,\frac{\partial^2 \mathcal{G}_2}{\partial n\partial n'}\,\frac{\chi'}{\rho'}\,ds\,ds'},$$

involving integrations only over the surface 3.

For comparison with the example of Carlson and Hendrickson[1], one notes that for that case

$$\rho = \text{const.},$$

$$\frac{1}{V_o}\frac{\partial V_1}{\partial n} = -1/\ell\ ,$$

$$G_2 = \frac{1}{2\pi\rho}\int \mathcal{G}_2\,d\phi\ ,$$

$$K_2 = \left[-1 - \pi b^2 \ell\,\frac{\partial^2 \mathcal{G}_2}{\partial n\partial n'}\right] \text{ at } z = \ell \text{ (i.e., at electrode 3),}$$

and $$\frac{\rho\ell}{\pi b^2} = R_o\ .$$

Hence, for the example chosen,

$$\frac{1}{R_{\ell.\ell.}} = \frac{1}{R_o} - \frac{1}{R_o}\;\frac{\left[\int \chi(r)\,r\,dr\right]^2}{\iint r\chi(r)\,[K_2(r,r') + 1]\,r'\chi(r')\,dr\,dr'}$$

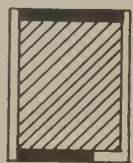
$$= \frac{1}{R_o}\;\frac{\iint r\chi(r)\,K_2(r,r')\,r'\chi(r')\,dr\,dr'}{\iint r\chi(r)\,K_2(r,r')\,r'\chi(r')\,dr\,dr' + \left[\int \chi(r)\,r\,dr\right]^2}$$

$$= \frac{1}{R_o}\;\frac{\Lambda}{\Lambda + 1},$$ in consistency with eq. (35) of the referenced paper (LR-132).

D. EXAMPLE

As an example consider the following "two dimensional" problem, which also may be solved rigorously by a simple Schwarz-Christoffel transformation when L is large:

A slab of homogeneous resistive material, of height h, extends from x = 0 to b and y = 0 to L. Current enters the specimen at y = L by an electrode extending from x = 0 to b and leaves at y = 0 by an electrode extending from x = 0 to a.



1. Upper limit:

In view of the two-dimensional character of this example, it suffices to use a Green's function, G_1, such that

(i) $\nabla^2_{x,y} G_1 = -\rho\,\delta\,(x, y; x', y')$,

(ii) $G_1 = 0$ at $y = L$, and

(iii) $\partial G_1/\partial n = 0$ on the other boundaries.

Then
$$R_{u.\ell.} = \frac{\iint J_n(x)\, G_1\,(x, x')\, J_n(x')\, dx\, dx'}{h\left[\int J_n(x)\, dx\right]^2} .$$

A suitable form for the Green's function will be

$$A_o\,(L-y') + \sum_1^\infty A_n \cos n\pi x/b \cosh n\pi y/b \sinh n\pi(L-y')/b, \text{ for } y < y' ;$$

$$A_o\,(L-y) + \sum_1^\infty A_n \cos n\pi x/n \sinh n\pi(L-y)/b \cosh n\pi y'/b, \text{ for } y > y' ;$$

with
$$\lim_{\varepsilon \to 0}\left[\left.\frac{\partial G_1}{\partial y}\right|_{y=y'-\varepsilon} - \left.\frac{\partial G_1}{\partial y}\right|_{y=y'+\varepsilon}\right] = \rho\ \delta\ (x-x') .$$

Accordingly, $A_o = \rho/b$,

$$A_n = \frac{2\rho}{\pi} \frac{\cos n\pi x'/b}{n \cosh n\pi L/b} \qquad (n \geqslant 1), \quad \text{and}$$

$$G_1(x, 0; x', 0) = \rho \left[\frac{L}{b} + \frac{2}{\pi} \sum_{1}^{\infty} \frac{1}{n} \cos n\pi x/b \cos n\pi x'/n \tanh n\pi L/b \right].^{4}$$

If one selects an assumed approximate distribution function J_n = const. $(0 < x < a)$ and performs the requisite integrations termwise,

$$R_{u.\ell.} = \frac{\rho \left[\frac{La^2}{b} + 2\frac{b^2}{\pi^3} \sum \frac{1}{n^3} \sin^2 n\pi a/b \tanh n\pi L/b \right]}{h a^2}$$

$$= \frac{\rho}{h} \left[\frac{L}{b} + \frac{2}{\pi^3} \frac{b^2}{a^2} \sum \frac{1}{n^3} \sin^2 n\pi a/b \tanh n\pi L/b \right], \quad \text{and}$$

for L large,

$$R_{u.\ell.} \simeq \frac{\rho}{h} \left[\frac{L}{b} + \frac{2}{\pi^3} \frac{b^2}{a^2} \sum \frac{1}{n^3} \sin^2 n\pi a/b \right].$$

The term supplementing $\frac{\rho L}{hb}$ represents the estimated addition to the resistance of the sample as a result of limiting the area of electrode number 2.

2. Lower Limit:

One again makes use of a two-dimensional Green's function, G_2, which is now required to satisfy the conditions:

(i) $\nabla^2_{x,y} G_2 = - \rho\, \delta(x, y; x', y')$,

(ii) $G_2 = 0$ at $y = 0$, $y = L$, and

(iii) $\frac{\partial G_2}{\partial x} = 0$ at $x = 0$, $x = b$.

[4] It should be remarked that Professor Carlson has pointed out that in this case the series may be summed, when L is large, to

$$G_1(x, 0{:}x', 0) \simeq \rho \left[\frac{L}{b} - \frac{1}{\pi} \ell n(2 \mid \cos\pi x/b - \cos\pi x'/b \mid) \right].$$

(Private communication.)

Then

$$\frac{1}{R_{\ell.\ell.}} = \frac{1}{R_o} + \frac{1}{L^2} \frac{h^2\left[\int \chi(x)\, dx\right]^2}{h \iint \chi(x)\left[\frac{\partial^2 G_2(x,y;x',y')}{\partial y\, \partial y'}\right]_{y,y'=0} \chi(x')\, dx\, dx'} .$$

or

$$R_{\ell.\ell.} = R_o - \frac{\rho^2}{hb^2} \frac{\left[\int \chi(x)\, dx\right]^2}{\iint \chi(x)\left[G_2'' + \frac{\rho}{Lb}\right] \chi(x')\, dx\, dx'} .$$

A formal expression for the Green's function may be written as

$$A_o\, y\,(L-y') + \sum_1^{\infty} A_n \cos n\pi x/b \sinh n\pi y/b \sinh n\pi (L-y')/b, \text{ for } y < y';$$

$$A_o\, y'\,(L-y) + \sum_1^{\infty} A_n \cos n\pi x/n \sinh n\pi (L-y)/b \sinh n\pi y'/b, \text{ for } y > y';$$

with $A_o = \dfrac{\rho}{Lb}$,

$$A_n = \frac{2\rho}{\pi} \frac{\cos n\pi x'/b}{n \sinh n\pi L/b} \qquad (n \geqslant 1) .$$

For a trial function, $\chi(x)$, one might prefer to employ a distribution which near the electrode is proportional to $\sqrt{x-a}$; for illustrative convenience, however, the function

$$\chi(x) = \frac{\pi}{2} \frac{x-a}{b-a}$$

is selected. By formal integration* in the case that L is large, one is led to the result

$$R_{\ell.\ell.} \simeq R_o + \frac{\rho}{2\pi h} \frac{1}{\sum_1^{\infty} n \frac{\cos^2 n\pi a/b}{\left[1-(2n\frac{b-a}{b})^2\right]^2}}, \text{ for a non-integral value of } \frac{b}{2(b-a)},$$

---

* Despite the poor performance, with respect to convergence, of the series for G_2'' it is felt that the character of the series obtained after the double integration warrants confidence in the result of proceeding formally in this manner (with the particular trial function selected).

and

$$R_{\ell.\ell.} \simeq R_o + \frac{\rho}{2\pi h} \frac{1}{m\frac{\pi^2}{16} + \sum\limits_{\substack{1 \\ n\neq m}}^{\infty} n \frac{\cos^2 n\pi a/b}{\left[1 - (2n\frac{b-a}{b})^2\right]^2}} ,$$

when $\frac{b}{2(b-a)}$ equals an integer, m .

3. Exact Solution:

As was mentioned in the introductory paragraph of section D, the present problem admits of a simple exact solution for L large. A suitable Schwarz-Christoffel transformation is[5]

$$W = \sin^{-1}\left[\frac{\sin\frac{1}{2}\frac{\pi z}{b}}{\sin\frac{1}{2}\frac{\pi a}{b}}\right] .$$

At large distances above the x-axis, the potential function is

$$V \simeq \frac{\pi}{2}\frac{y}{b} - \ell n \sin\frac{\pi a}{2 b}$$

and the change of the stream function in traversing the electrode is

$$\Delta U = \frac{\pi}{2} .$$

Accordingly, the exact resistance for L large is

$$R \simeq \frac{\rho}{h}\left[\frac{L}{b} - \frac{2}{\pi}\ell n \sin\frac{\pi a}{2b}\right] .$$

4. Numerical Results:

Values for the supplemental resistance, obtained from the approximate formulas by numerical summation, are given in Table I.

[5] W.R. Smythe, l.c., sect. 4.22, pp. 90-91.

TABLE I

Values of the Supplemental Resistance, $R-R_o$, in units $\rho/2\pi h$.

	$R_{u.\ell.}$	$R_{\ell.\ell.}$	R_{exact}
Trial Function	J_n = const.	$\chi = \sin \frac{\pi}{2}\frac{x-a}{b-a}$	- - -
a/b = 1/4	4.26	3.04	3.842
a/b = 1/2	1.70	1.15	1.386
a/b = 3/4	0.39_2	0.26_8	0.317

APPENDIX I

Proof of the theorem that the current distribution is such that the "heating," $\iiint \rho J^2 \, d\tau$, is a minimum for fixed total current:

Let $\vec{J}_o$ be the correct current distribution, and $\vec{J}$ any other solenoidal current distribution corresponding to the same total current, I, at the electrodes.

Then (i) $\operatorname{div} \vec{J}_o = 0 = \operatorname{div} \vec{J}$,

(ii) $\iint \vec{J}_o \cdot \vec{ds} = \pm I = \iint \vec{J} \cdot \vec{ds}$, and

(iii) $\rho \vec{J}_o$ is derivable from a potential:

$\rho \vec{J}_o = -\overrightarrow{\operatorname{grad} V}$, with V constant on the electrodes.

It then follows that

$$\iiint \rho (J^2 - J_o^2) \, d\tau \equiv 2 \iiint \rho \vec{J}_o \cdot (\vec{J}-\vec{J}_o) \, d\tau + \iiint \rho (\vec{J}-\vec{J}_o)^2 \, d\tau$$

$$\equiv -2 \iiint (\overrightarrow{\operatorname{grad} V}) \cdot (\vec{J}-\vec{J}_o) \, d\tau + \iiint \rho (\vec{J}-\vec{J}_o)^2 \, d\tau$$

$$\equiv -2 \iiint \operatorname{div} [\, V(\vec{J}-\vec{J}_o) \,] \, d\tau + 2 \iiint V \operatorname{div}(\vec{J}-\vec{J}_o) \, d\tau$$

$$+ \iiint \rho (\vec{J}-\vec{J}_o)^2 \, d\tau$$

$$\equiv -2 \iint V(\vec{J}-\vec{J}_o) \cdot \vec{ds} + 2 \iiint V \operatorname{div}(\vec{J}-\vec{J}_o) \, d\tau$$

$$+ \iiint \rho (\vec{J}-\vec{J}_o)^2 \, d\tau$$

$$= \iiint \rho (\vec{J}-\vec{J}_o)^2 \, d\tau \geqslant 0 \, ,$$

and the heating is least for the correct current distribution.

APPENDIX II

Proof of the theorem that the potential distribution is such that the heating, $\iiint (1/\rho)(\text{grad } V)^2 \, d\tau$, is a minimum for a fixed interelectrode potential difference:

Let V_o be the correct potential distribution, for which

(i) $\text{div}\left(\frac{1}{\rho} \text{ grad } V_o\right) = 0$,

(ii) V_o assumes the prescribed potentials at the electrodes,

and (iii) $\partial V_o / \partial n = 0$ on the other boundaries.

V is taken to correspond to the same potential difference between the electrodes and, for convenience, might be considered to assume the same values as V_o on the electrodes. It then follows that

$$\iiint \frac{(\nabla V)^2 - (\nabla V_o)^2}{\rho} \, d\tau \equiv 2 \iiint \frac{\nabla V_o \cdot \nabla (V - V_o)}{\rho} \, d\tau + \iiint \frac{[\nabla (V - V_o)]^2}{\rho} \, d\tau$$

$$\equiv 2 \iiint \text{div} \left[(V - V_o) \frac{\text{grad } V_o}{\rho} \right] d\tau$$

$$-2 \iiint (V - V_o) \, \text{div} \left(\frac{1}{\rho} \text{ grad } V_o\right) d\tau$$

$$+ \iiint \frac{[\nabla (V - V_o)]^2}{\rho} \, d\tau$$

$$\equiv 2 \iint \frac{V - V_o}{\rho} \frac{\partial V_o}{\partial n} \, ds - 2 \iiint (V - V_o) \, \text{div}\left(\frac{\text{grad } V_o}{\rho}\right) d\tau$$

$$+ \iiint \frac{[\nabla (V - V_o)]^2}{\rho} \, d\tau$$

$$= \iiint \frac{[\nabla (V - V_o)]^2}{\rho} \, d\tau \geq 0,$$

and the heating is least for the correct potential distribution.

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REVIEW OF EPHEMERIDAE (EPHEMEROPTERA) IN THE MISSOURI RIVER WATERSHED WITH A KEY TO THE SPECIES[1]

E. W. Hamilton[2]

This paper deals with the mayflies of the Missouri River watershed; a watershed draining all or parts of the states of Montana, Wyoming, Colorado, North Dakota, South Dakota, Nebraska, Kansas, Iowa, and Missouri. Since specimens of mayflies were not obtained from South Dakota, this state is not included in the present study.

Specimens have been returned to the respective institutions from which they were borrowed. The material from Nebraska is being retained in the Entomology division of the Nebraska State Museum at the College of Agriculture. With extremely few exceptions, the records listed for a state are preserved at institutions in that state.

A proposed reclassification of the order by Edmunds and Traver (1954) is reminiscent of the one followed by Spieth (1933), but until the reasons for this grouping are forthcoming, it seems advisable to follow a more generally used classification such as is used by Needham, Traver, and Hsu (1935) or Burks (1953). Burks' arrangement of the Ephemeridae is identical to that proposed by Needham, except that the Neoephemera of Needham is placed in a new family, Neoephemeridae. Neoephemerids have not been found in the Missouri River Basin. The subfamilies of the Ephemeridae recognized by Burks are Campsurinae, Ephorinae, Potamanthinae, Ephemerinae, and Palingeniinae, an exotic group.

The 100th meridian, which traverses the middle of the Dakotas and the western portions of Nebraska and Kansas, is apparently the approximate geographical limit of many species of eastern and western Ephemeroptera. Examples of this limitation will be noted in the discussion of the species involved.

EPHEMERIDAE

Ephemerids are medium to large mayflies that include the largest representatives of the Ephemeroptera. Their wings have numerous cross-veins and, except in the Campsurinae, a network of marginal veinlets (Figs. 3-8). Veins Cu_1 and M_2 in the basal area of the fore wing curve strongly away from the nearly straight veins M_1 and R_4+R_5 (Figs. 3-8). In all other mayfly families (except Neoephemeridae) Cu_1, M_2, M_1, and R_4+R_5 of the fore wing are nearly straight or only moderately curved and but slightly divergent in the basal area (Figs. 1, 2). Veins R_4 and R_5

[1] This study was made while the author was a member of the Department of Entomology, University of Nebraska. Published with the approval of the Director as Paper No. 756, Journal Series, Nebraska Agricultural Experiment Station.

[2] Published while in residence at Iowa State College.

of the ephemerids are fused in the hind wing and form a fork in the fore wing. The uniformly faceted compound eyes are usually divided by a nearly horizontal line into dark and light areas of equal size. In Ephorinae and Campsurinae, the middle and hind legs are either extensively reduced or absent; in the other subfamilies the legs are normally developed. Male fore tarsi are five-segmented with the basal tarsal segment very short. All hind tarsi of both sexes have four freely movable segments with the almost indiscernible fifth segment fused to the tibia.

In all species, the nymphs (Figs. 29, 30) have mandibular tusks (Figs. 29-30) and biramous plume-like gills on abdominal segments 1-7 (Figs. 37-40) that are held in either a dorsal or lateral position. Most species have a frontal process (Figs. 30-36) on the head. Nymphs of this family are generally digging forms that sprawl or bury themselves in the silt and fine sand of the larger lakes and rivers.

Key to the Species

Adults

Subfamily differentiation, which is based on wing venation and genitalic differences is relatively simple. Separation of the species is based in great part on color patterns and male genitalia. Intraspecific color variation is pronounced in the species of Hexagenia and the key couplets for this genus are workable only for typical specimens.

1. Median caudal filament as long as or longer than distance from segment 8 to base of filament 2
   Median caudal filament vestigial, much shorter than distance from segment 8 to base of filament. 8
2. Hind tibia longer than femur; wings normally with a variable pattern of dark spots (Figs. 6, 7) (Ephemerinae) 3
   Hind tibia shorter than femur; wings without dark spots or blotches. 5
3. Sterna unmarked; terga with a dark median band (Fig. 28); usually four black spots from bulla posteriorly across wing (Fig. 7); penes tube-like (Fig. 12). . . . . Pentagenia vittigera
   Dark markings on sterna; terga with dark marks, but not as above; dark spotting on wings more extensive (Fig. 6); penes short, truncate (Fig. 13). 4
4. Paired, subparallel, longitudinal, black, linear streaks on abdominal terga 3-8; black submedian streaks on each sterna. Ephemera compar
   Large dark blotches laterally on each abdominal terga; dark, oblong, submedian triangles on each sterna. . Ephemera simulans
5. Cubital intercalaries simple, four long; wing heavily cross-veined (Fig. 4) (Ephorinae).... female . . . . . Ephoron album
   Cubital intercalaries one or two, long and deeply forked; wing less heavily veined (Fig. 5) (Potamanthinae). 6
6. Eyes of male separated by 2.5 times width of eye as seen from above; cross-veins of fore wing pale in both sexes. 7

Eyes of male separated approximately by width of eye; cross-veins of female fore wing blacksih, of male hyaline. . . . . Potamanthus verticis

7. Lateral dusky pink spots on each abdominal tergite. . . . . Potamanthus rufus
Lateral spots very rarely present. . . . . . Potamanthus myops

8. Marginal veinlets absent (Campsurinae)(Fig. 3). Tortopus primus
Marginal veinlets present. 9

9. Four long, unforked cubital intercalaries (Fig. 4); penes strongly divergent apically, truncate (Fig. 10). . . . male. . . . . Ephoron album
Short, shallow forked cubital intercalaries, more like marginal veinlets; genitalia not as above (Ephemerinae) . . . 10

10. Sterna with a narrow median streak (Figs. 22b, 24b). 11
Sterna not marked as above. 12

11. Median streaks present on abdominal terga 3-6 (Fig. 22a). . . . . Hexagenia limbata limbata
Median streaks absent on abdominal terga 3-6 (Fig. 24a). . . . . Hexagenia limbata venusta

12. Triangular areas medially on abdominal sterna (Fig. 23b). . . 13
Markings on abdominal sterna not triangular. 15

13. Markings on abdominal terga 3-6 very dark (Fig. 23a); penes as in Fig. 15 . . . . Hexagenia limbata occulta
Markings on abdominal terga lighter; penes not as above . . . 14

14. Markings on abdominal terga 3-6 as in Fig. 27a; penes long, slender (Fig. 17). . . . . Hexagenia rigida
Markings on abdominal terga 3-6 chevron-like (Fig. 20); penes short, broad (Fig. 14). . . . . Hexagenia atrocaudata

15. Truncate triangular markings on sterna (Figs. 25b, 26b); penes similar to those of H. limbata (Fig. 16). 16
Sterna not marked as above; penes otherwise. 17

16. Abdominal terga 3-6 dark medially (Fig. 25a). . . . . Hexagenia munda affiliata
Abdominal terga 3-6 pale medially (Fig. 26a). . . . . Hexagenia munda munda

17. Abdominal sterna 3-6 broadly dark-banded, usually with a lighter median triangular area (Fig. 21b); penes beak-like (Fig. 19). . . . . Hexagenia bilineata
Abdominal sterna 3-6 light with diffuse markings (Fig. 27b); penes long, slender, almost straight (Fig. 17). . Hexagenia rigida

Nymphs

Many of the ephemerid nymphs are either undescribed or have been difficult to associate accurately with adults. The following key (couplets 6-9 modified from Burks, 1953) is given as an aid to identification of the known nymphs.

1. Frontal process absent (Fig. 29). 2
Frontal process present (Figs. 30-36) 3

2. Fore tibia slender and longer than femur (Fig. 29). . Potamanthinae
   Fore tibia almost as broad and flat as, and shorter than, the femur (Fig. 30). . . . . Campsurinae
3. Frontal process bifid (Figs. 32, 33). 4
   Frontal process varying but not bifid. 5
4. Mandibular tusks crenate on outer margin (Fig. 32); labial palp 2-segmented. . . . . Pentagenia vittigera
   Mandibular tusks smooth on margins (Fig. 33); labial palp 3-segmented. . . . . Ephemera spp.
5. Frontal process truncate, often slgihtly emarginate (Fig. 34). . . . . Hexagenia atrocaudata
   Frontal process apically rounded or angled. 6
6. Mandibular tusks converging; frontal process conical (Fig. 31). . . . . Ephoron album
   Mandibular tusks diverging; frontal process not as above. . . . 7
7. Frontal process rounded (Fig. 30). . . . . . . Hexagenia limbata
   Frontal process conical or apically angled. 8
8. Frontal process as in Fig. 35; mid-tarsal claw thick near tip (Fig. 41). . . . . Hexagenia bilineata
   Frontal process apically angled but not as above; mid-tarsal claw slender near tip. 9
9. Mid-tarsal claw long and slender (Fig. 43). . . . . Hexagenia rigida
   Mid-tarsal claw slender near tip, broad at base (Fig. 42). . . . . Hexagenia munda

Subfamily Campsurinae

Species of this subfamily are superficially similar to the Ephorinae. However, the following venational characters differ from those found in other Ephemeridae: marginal veinlets lacking in both wings; Sc and R_1 of the fore wing curving around the apical edge of fore wing; and fork R_4+R_5 of the fore wing longer than fork R_2+R_3 (Fig. 3).

Tortopus Needham and Murphy, and Campsurus Eaton are the only generic representatives of this subfamily in the Nearctic Region. Although these two genera are well represented in Central and South America, only four species are found in America north of Mexico. Species of Campsurinae in North America not found in the Missouri River watershed are Campsurus decoloratus (Hagen) from Texas, C. circumfluus Ulmer from Texas, and C. puella (Pictet) from Louisiana. C. puella may fall as a synonym of T. primus when it can be studied more carefully.

Tortopus Needham and Murphy

Tortopus Needham and Murphy, 1924, 23: Burks, 1953, 28.

This genus differs from Campsurus in that the middle and hind legs of Tortopus are complete, although reduced in size, while those of Campsurus are absent beyond the trochanter. There are also some differences in wing venation that are not reliable (Ulmer, 1942).

The nymphs of Tortopus are unknown.

Type of genus: Tortopus igaranus Needham and Murphy (by original designation).

Tortopus primus (McDunnough)

Campsurus primus McDunnough, 1924a, 7; Needham and Murphy, 1924, 15; McDunnough, 1926, 185 (in discussion of C. puella Pictet); Needham, Traver, and Hsu, 1935, 287.

Campsurus incertus Traver, 1935 (in Needham, Traver, and Hsu), 286; Berner, 1950, 97.

Campsurus manitobensis Ide, 1941, 155.

Tortopus primus, Burks, 1953, 28.

An examination of the types of T. primus indicates that Burks' (1953) synonymy for this species is accurate. In the holotype and paratypes the genitalia appears as in Fig. 18. Mrs. L. K. Gloyd (Ill. Nat. Hist. Survey), after examining a series of 75 pinned specimens bearing the same accession number as the types, states in correspondence, "If one rotates the tip of the (genital) structure about 60°, turning the beak-like point toward you, you get Burks' (1953) view as in (his) Fig. 60. Now turn the 'beak' downward a little, as would happen if the two mesal processes (penes) were brought closer together, and then draw the outline of the shrunken inside tissue and you have McDunnough's figure—especially if in inking it you would let your pen go to the outside of your original sketch of the tip." Her viewpoint agrees with and confirms that held by the author of this paper. In the same manner, it is possible that the slight genitalic variance mentioned by Ide (1941) in his description of C. manitobensis is a result of a different deformation of the genitalia caused by drying and shrinkage. Burks' (1953) synonymy of C. manitobensis and T. primus is thus also believed to be correct although no reason was given by Burks for the synonymy.

Recorded distribution: Alabama, Arkansas, Florida, Georgia, Illinois, Kansas, Manitoba, Missouri, Nebraska, Ontario, Tennessee, and Texas.

New records: IOWA, Story Co., Ames - 1♂. KANSAS, Osborne, Co., Osborne - 1♂. NEBRASKA, Buffalo Co., Kearney (G. Edmunds); Dawson Co., Cozad, 29-VII-1949, at light (E. W. Hamilton) - 5 ♀♀; Madison Co., Monroe, 18-VI-1950, at Tri-County canal (E.B. Burcham) - 11 ♀♀.

Note: All known records are east of the 100th meridian.

Ephorinae

This group superficially resembles the Campsurinae. Only one genus, Ephoron Williamson, is present in North America.

The generic name Ephoron is derived from a neuter Greek adjective which in Latinized form is ephorum or ephorus. Ephori is the genitive of ephoron; hence the correct spelling of the subfamily name is Ephorinae. The spelling Ephoroninae is to be regarded as a lapsus calami and corrected.

Ephoron Williamson

Ephoron Williamson, 1802, 71; Ulmer, 1932, 205-8; Needham, Traver, and Hsu, 1935, 241; Ide, 1935, 113; Lestage, 1938, 381-94; Spieth, 1940, 109-111; Burks, 1953, 32.
Polymitarcys Eaton, 1868, 84; Eaton, 1871, 60; Eaton, 1883, 43; Ulmer, 1920, 209; Needham, 1920, 288; Spieth, 1933, 347.

McDunnough (1926) synonymized Polymitarcys Eaton and Ephoron Willaimson, a synonymy that has been accepted by the majority of present-day ephemeropterists. Spieth (1940) gives a very able and conclusive discussion of the evidence involved.

Only two species of this genus are found in North America, Ephoron album (Say) and E. leukon Williamson. E. leukon is an eastern species.

In the species of Ephoron, each wing is profusely cross-veined and bordered posteriorly with a net-like series of marginal veinlets (Fig. 4). As in Tortopus, the posterior two pairs of legs are reduced and useless.

Nymphs of both species have been described.

Type of genus: Ephoron leukon Williamson (by monotypy).

Ephoron album (Say)

Baetis alba Say, 1823, 305; Hagen, 1863, 170; Eaton, 1871, 124.
Palingenia alba, Hagen, 1861, 40.
Polymitarcys albus, Hagen, 1873, 391; Eaton, 1883, 47; Banks, 1894, 178; Howard, 1905, 60; Needham, 1920, 285.
Ephoron album, McDunnough, 1926, 184; Needham and Christenson, 1927, 16; Neave, 1932b, 54; Ide, 1935, 113 (in discussion); Needham, Traver, and Hsu, 1935, 243; Spieth, 1940, 110 (in discussion); Edmunds, 1948, 12; Burks, 1953, 35.
Cloe sp. (A), Walsh, 1863, 191 (synonymy after Traver, 1935).

Edmunds (1948) described and figured the nymph of this species.
Recorded distribution: Illinois, Iowa, Kansas, Ohio, Utah, and Washington.
New records: IOWA, Story Co., Ames (Quayle) - 2 ♀♀ ; Henry Co., Mt. Pleasant, 24-IX-1935 (C. Horn) - 1♀ , 14-VII-1949 (C. Yoshimoto) - 1 ♀. KANSAS, Douglas Co., August, at light (U. of Kan. Col. Lots 83 and 91) - 7 ♀♀ ; Ellis Co., 19-VII-1912, 2000 feet (F.X. Williams) - 7 ♂♂ (with the following additional label "Polymitarcys alba Say, Det. Nathan Banks" on two specimens). MONTANA, Gallatin Co., 23-XI-1947, Madison-Jefferson Rivers near junction with Gallatin River (R.A. Hayes) - ♂♂ . NEBRASKA, Cherry Co., Snake River Falls, 5-VIII-1948, Snake River (M.H. Muma) - 1 nymph; Dawson Co., Cozad, 15-VI-1950, at light (E.W. Hamilton) - 2 ♂♂, 12♀♀; Dundy Co., Rock Creek Hatchery; Frontier Co., Curtis, 2-VIII-1949, light trap (J. Lomax) - 11♀♀; Scotts Bluff Co., Scottsbluff, 27-IX-1951, at canal (E.W. Hamilton) - 6♂♂, 4 ♀♀; Sioux Co., University Lake, 25-VIII-1949, at light (E. Laird) - 3 ♀♀.

Potamanthinae

The subfamily Potamanthinae is represented by only one Nearctic genus.

Potamanthus Pictet

Potamanthus Pictet, 1845, 197; Eaton, 1868, 86; Eaton, 1871, 76; Eaton, 1884, 78; Banks, 1907, 16; Morgan, 1911, 99; Needham, 1920, 287; Ulmer, 1920, 110; Argo, 1927, 320; Spieth, 1933, 345; Needham, Traver, and Hsu, 1935, 277; Ide, 1935, 117; Berner, 1950, 79; Burks, 1953, 30.

Mayflies belonging to this genus are the smallest species of the Ephemeridae. Burks (1953) writes, "Adult specimens of Potamanthus should be studied when freshly killed, as the faint color markings fade rapidly after death." Genitalia of all species are nearly identical in form (Fig. 11). There is no good method for distinguishing the females. The nymphs of this genus have not been satisfactorily separated.

Type of genus: Ephemera luteus Linnaeus (by subsequent selection, Eaton, 1868).

Potamanthus myops (Walsh)

Ephemera myops Walsh, 1863, 207; Eaton, 1871, 71; Eaton, 1883, 72; Banks, 1907, 16.

Potamanthus myops, McDunnough, 1926, 186; Argo, 1927, 320, 322, 323; Needham, Traver, and Hsu, 1935, 281; Burks, 1953, 31.

Potamanthus medius Banks, 1908, 259; McDunnough, 1926, 186; Argo, 1927, 321; Needham, Traver, and Hsu, 1935, 281. (Synonymy after Burks, 1953).

See remarks under P. rufus Argo regarding possible synonymy of rufus and myops.

The nymph has not been described.

Recorded distribution: Illinois, Indiana, Iowa, Kansas, Michigan, and Wisconsin.

Note: All records are east of the 100th meridian.

Potamanthus rufus Argo

Potamanthus rufus Argo, 1927, 323; Ide, 1935, 121; Needham, Traver, and Hsu, 1935, 282.

Specimens from Kansas and Missouri have been identified, possibly in error, as P. rufus. Besides having the lateral dusky spots, as in P. rufus, the Missouri specimens (all subimagoes) also have lateral dusky shading on the abdominal terga distinctly visible from above as a continuous band, but almost indiscernible on most individuals in the lateral view. The lateral abdominal spots on the imagoes from Kansas look more like faint, short dashes.

P. rufus is closely related to P. myops with only slight differences between them being noted by Argo (1927). P. inequalis Needham (1908), another form that apparently represents an intermediate condition between P. rufus and P. myops, is, as McDunnough (1926) mentions, "... very close to, if not identical with, myops Wlsh.;"

In his redescription of P. myops, Burks (1953) states, "abdomen without lateral, salmon-pink spots or stripes, or, rarely, with small, faint, lateral spots discernible in living specimens;" Needham (1908) in speaking of P. inequalis mentions "faint opaque brownish areas on each tergite, and Argo (1927) in his characterization of P. rufus describes "fuscous spots" laterally on each tergite. The genitalia of each species is nearly identical. It is possible that a comparison of the types of these three species would indicate that there is actually only one species.

A nymphal description is given by Ide (1935).

Recorded distribution: New York, Ontario.

New records: KANSAS, Douglas Co., June, at light (U. of K. Col. Lot 47) - 1♀; July, at light (U. of K. Col. Lots 64, 67, 69, 71, 81) - 3♂♂, 13♀♀. MISSOURI, Pike Co., Louisiana, 15-VI-1953, at light, - 32♂♂, 9♀♀, all subimagoes.

Note: All records are east of the 100th meridian.

Potamanthus verticis (Say)

Baetis verticis Say, 1839, 42; Walker, 1853, 562; Hagen, 1861, 46; Walsh, 1863, 204 (in discussion); Eaton, 1871, 121.

Ecdyurus verticis, Eaton, 1885, 278.

Heptagenia verticis, Banks, 1907, 21; Banks, 1910, 201.

Potamanthus verticus, McDunnough, 1926, 186; Needham, Traver, and Hsu, 1935, 283; Berner, 1953, 31.

Ephemera flaveola Walsh, 1862, 377; Hagen, 1863, 178; Eaton, 1871, 70; Eaton, 1883, 71. (synonymy after McDunnough, 1926).

Heptagenia flaveola, Eaton, 1871, 149.

Potamanthus flaveola, Banks, 1907, 16; Needham, 1920, 287; Ide 1935, 119, 120.

Potamanthus bettini, Morgan, 1913, Pl. XLIV, Fig. 7 (in part-nymph only).

Argo's (1927) specimens (erroneously identified as P. verticis) belong to the species P. neglectus Traver (1935). The large eyes of P. verticis are markedly different from the small eyes of P. neglectus.

On each tergite of the specimens from Missouri, is a lateral dot with an arched to triangular mark above. Traver (1935) mentions these same markings. A lateral dusky shading similar to that described on specimens of P. rufus is also present.

Nymphs of P. verticis have been described or figured by Morgan (1913, P. bettini), Needham (1920, P. flaveola), and Ide (1935, P. flaveola).

Recorded distribution; Hudson Bay, Illinois, Indiana, Michigan, New York, Ontario, and Tennessee.

New records: MISSOURI, Pike Co., Louisiana, 15-VI-1953, at light - 7♂♂,, 10♀♀,, all subimagoes.

Note: All records are east of the 100th meridian.

Ephemerinae

Pentagenia Walsh

Pentagenia Walsh, 1863, 196; Eaton, 1868, 85; Eaton, 1883, 75; Ulmer, 1920, 109; Needham, 1920, 282; Spieth, 1933, 347; Needham, Traver, and Hsu, 1935, 255; Burks, 1953, 37.

Only two species of this genus are known in North America; one of them is found in the area studied. Their life histories are unknown.

Type of genus: Palingenia vittigera Walsh (by subsequent selection - Eaton, 1868).

Pentagenia vittigera (Walsh)

Palingenia vittigera Walsh, 1862, 373; Hagen, 1863, 174.
Pentagenia vittigera Walsh, 1863, 197; Eaton, 1868, 85; Eaton, 1871, 63; Eaton, 1883, 76; Needham, 1920, 282; McDunnough, 1926, 185; Needham, Traver, and Hsu, 1935, 257; Berner, 1950, 96; Burks, 1953, 37.
Pentagenia quadripunctata Walsh, 1863, 198; Eaton, 1871, 64; Eaton, 1883, 77; Banks, 1894, 178. (synonymy after Needham, 1920).

At the time of his erection of the genus Pentagenia, Walsh (1863) described two forms, P. vittigera and P. quadripunctata. Needham (1920) considered P. quadripunctata "only a variant." His synonymy has been generally accepted.

The nymph has been described by Needham (1920) and Spieth (1941).

Recorded distribution: Alabama, Arkansas, Florida, Illinois, Indiana, Iowa, Kansas, Manitoba, Missouri, Tennessee, and Texas.

New records: IOWA, Clinton Co., Clinton, 28-VIII-1943 (D.T. Jones) - 2 ♀♀; Des Moines Co., Burlington, 14-VIII-1925 (H.M. Harris) - 1♀, 20, 21-VI-1951 (Newby) - 2 ♀♀; Dickinson Co., 10-VIII-1939 (H. E. Jaques) - 1♀; Henry Co., Mt. Pleasant, 24-IX-1935 (C. Horn) - 1 ♀, 18-VI-1938 (M. Cornick), 19-VII-1939) (Staebler), 13-VII-1948 (S. Statler), 20-VI-1949 (Donovan Orman), 14-VI-1941 (B.J. Luke), 23-VI-1951 (Widmer), 2-VII-1941 (Ben Luke) - 3 ♂♂, 7 ♀♀; Muscatine Co., 12-VI-1936 and 22-VI-1937 (Bernard Berger) - 1♂, 1♀; Van Buren Co., 14-VIII-1949 (M. Schwabauer) - 1♀, Keosauqua, 1-IX-1953, at light (W.S. Craig) - 1♀; Washington Co., 2-VIII-1947 (Toker) - 2 ♀♀. KANSAS, Douglas Co., June (U. of K. Col. Lots 43, 58) - 1♀, July, (U. of K. Col. Lot 69) - 1♀ subimago, July, (U. of K. Col. Lot 83) - 1♀, August, (U. of K. Col. Lot 97) - 1 ♀ subimago (all taken at lights); Douglas Co., Lawrence, 25-V-1922, at light (W.J. Brown) - 1 ♂ subimago. MISSOURI, Boone Co., Columbia, 15-VIII-1953, at lights (W. R. Enns) - 1♀; Lincoln Co., Clarksville, 15-VI-1953, at light - about 30 imagoes, subimagoes, both sexes; Pike Co., Louisiana, 15-VI-1953, at light - about 100 imagoes, subimagoes, both sexes. NEBRASKA, Madison Co., Norfolk, 10-VIII-1949, at light (R.E. Hill) - 1♀; Platte Co., Columbus, 2-VII-1950, at light (E.W. Hamilton) - 5 ♂♂, 4 ♀♀. WISCONSIN, Dane Co., 20-VII-1947 - 1 ♀.

Note: All records are east of the 100th meridian.

Ephemera Linnaeus

Ephemera Linnaeus, 1758, 546; Leach, 1815, 137; Eaton, 1868, 85; Eaton, 1871, 68; Eaton, 1883, 58; Ulmer, 1920, 109; Needham, 1920, 283; Spieth, 1933, 347; Needham, Traver, and Hsu, 1935, 246; Burks, 1953, 35.

Type of genus: Ephemera vulgata Linnaeus (by subsequent selection, Eaton, 1868).

Ephemera compar Hagen

Ephemera compar Hagen, 1875, 578; Eaton, 1883, 65; Needham, Traver, and Hsu, 1935, 249.

This species has not been collected since the original description. Traver (1935) writes "it is apparently close to E. simulans, but slightly larger."
Recorded distribution: Colorado.

Ephemera simulans Walker

Ephemera simulans Walker, 1853, 536; Hagen, 1863, 38; Eaton, 1883, 67; Needham, 1908, 261; Morgan, 1911, 100; Clemens, 1913, 332; Clemens, 1915, 116; Ide, 1930, 206; Needham, Traver, and Hsu, 1935, 252; Spieth, 1940, 325, 326, 327; Berner, 1950, 94; Burks, 1953, 36.
Palingenia natata Walker, 1853, 551.
Ephemera natata, Hagen, 1863, 39; Hagen, 1863, 177; Hagen, 1873, 384; Hagen, 1875, 580. (synonymy after Eaton, 1883)
Ephemera decora Walker, 1853, 536; Walsh, 1862, 376; Hagen, 1863, 177. (synonymy after Eaton, 1883)
Ephemera varia, Needham, 1920, 271 (in part—nymph only).

The nymph has been described and figured by Needham (1920) and incorrectly identified as E. varia.
Recorded distribution: Alberta, Colorado, Connecticut, Florida (?), Hudson Bay, Idaho, Illinois, Maine, Manitoba, Michigan, Minnesota, Montana, New York, Ohio, Ontario, Pennsylvania, Saskatchewan, Utah, Virginia, and Wyoming.

Hexagenia Walsh

Hexagenia Walsh, 1863, 197; Eaton, 1868, 85; Eaton, 1871, 64; Eaton, 1883, 48; Ulmer, 1920, 108; Needham, 1920, 278; Ulmer, 1921, 233; McDunnough, 1924b, 90; Traver, 1931, 591; Lestage, 1931, 39; Spieth, 1933, 347; Needham, Traver, and Hsu, 1935, 258; Spieth, 1941, 233; Berner, 1950, 78; Burks, 1953, 38.

The great color variations within and small genitalic differences between the species of this genus have caused universal confusion in the taxonomy of this group. Because of this confusion many synonyms have

been incorrectly applied. At various times Hagen (1861, 1863), Eaton (1871, 1883), and Needham (1920) placed H. limbata and its subspecies H. l. limbata, H. l. occulta, H. l. venusta, and H. l. viridescens as synonyms of H. bilineata. Needham (1920), for example, wrote, "A good many names have been applied to the different forms of this genus, but after a careful study of a good bit of material from many localities I am unable to recognize more than two good and distinct species in the eastern United States—a lowland species from lakes and rivers, Hexagenia bilineata Say, and an upland bog-species, H. recurvata Morgan." However, Walsh (1863) considered H. limbata and H. bilineata distinct at the time he described this genus. On other occasions authorities such as Walker (1853), Eaton (1883), McDunnough (1924, 1927), and Traver (1931, 1935), though usually lacking large series of specimens, took the opposite view and described many species on the basis of slight color and genitalia variations.

Spieth in 1941 proposed a much needed revision of this genus relegating several species to subspecific rank and synonymizing many others. He thus reduced the 18 Nearctic species of Traver (1935) to 6 species and 10 subspecies. Though agreeing in general with Spieth's (1941) revision, Burks (1935) did not recognize Spieth's "subspecific segregates within the species limbata and munda."

Type of genus: Ephemera limbata Serville (by subsequent selection, Eaton, 1868). Eaton (1883) in a later paper contradicted his original type selection by listing Baetis bilineata Say as the type of the genus. Traver (1935) and Spieth (1941) apparently overlooked Eaton's earlier (1868) paper and erroneously followed the later type selection given by Eaton in 1883.

Hexagenia atrocaudata McDunnough

Hexagenia atrocaudata McDunnough, 1924b, 92; McDunnough, 1927, 117; Traver, 1931, 611; Needham, Traver, and Hsu, 1935, 262; Spieth, 1941, 240; Burks, 1953, 39.

Contrary to the usual wide specific color variation encountered in this genus, this species (Spieth, 1941) has a "remarkably constant" color pattern.

The nymph has been described by Traver (1931).

Recorded distribution: Georgia, Illinois, Indiana, Maryland, Michigan, Missouri, New York, North Carolina, Ohio, Ontario, Pennsylvania, Virginia, and West Virginia.

Note: All records are east of the 100th meridian.

Hexagenia bilineata (Say)

Baetis bilineata Say, 1824, 303.

Palingenia bilineata, Hagen, 1861, 41; Walsh, 1862, 373; Hagen, 1863, 174; Walsh, 1863, 199-202.

Hexagenia bilineata, Eaton, 1871, 66; Eaton, 1883, 50; Clemens, 1913, 331; Needham, 1920, 278; Ulmer, 1921, 235; McDunnough, 1924b, 90; Wiebe, 1926, 267; McDunnough, 1927, 116; Traver, 1931, 591 (in

discussion), 611 (in key), 615 (nymph); Traver, 1937, 76; Needham, Traver, and Hsu, 1935, 263; Spieth, 1941, 242; Berner, 1950, 93; Burks, 1953, 38.

This is a very dark species whose abdomen, in the lateral view, appears to be striped. Darker markings may completely obscure the paler median ventral triangles (Fig. 21b). H. limbata occulta has often been confused with this species but the abdominal markings (Fig. 23) and genitalia (Fig. 15) of H. l. occulta are quite different from that of H. bilineata (Figs. 18, 21).

Baetis angulata Walker, at one time listed as a synonym of H. bilineata by Eaton (1883), is discussed under the subspecies H. limbata occulta.

The nymph has been described by Needham (1920) and Traver (1931).

Recorded distribution: Alabama, District of Columbia, Georgia, Illinois, Indiana, Iowa, Kentucky, Lousiana, Maryland, Minnesota, Mississippi, Missouri, New Mexico, Ohio, Oklahoma, Tennessee, Texas, and Virginia.

New Records: IOWA, Butler Co., 6-VII-1940 (U.W.) - 1♂; Des Moines Co., Burlington, 4-VIII-1926 (H.M. Harris) - 2♀♀; Henry Co., Mt. Pleasant, 4-VII-1928 and 11-VII-1928 (Van Horn), 16-VII-1930 (H. Knight), 15-VII-1942 (A. Pidgeon) - 4♀♀, 13-VII-1948 (S. Statler) - 1♀, 18-VI-1949 (C. Yoshimoto) - 1♀, 20-VI-1949 (Orman Donovan) - 1♂ (very pale), 25-VI-1949 (P. Kautsky) - 1♀, 19-VII-1951 (Newby) - 2♀♀, 20-VII-1941 (Miller) - 1♀, 25-VII-1951 (R. Newby) - 1♀, 31-VII-1951 (Clegg) - 1♀ (D. Prickett) - 1♀; Lee Co., 24-VII-1929 (Farris) - 1♀; Muscatine Co., Muscatine, 12-VII-1894 (H.C.) - 2♀♀, 14-VI-1934 (H.E. Jaques) - 1♀ (subimago), 4-VII-1951 (Newby) - 1♂ (subimago); Scott Co., LeClaire 2♀♀. KANSAS, Douglas Co., 7-VII-1920 and 9-VII-1920 (William E. Hoffman) - 4♀♀; Riley Co., Manhattan, 2-VII-1949 (L. Edelblute) - 2♀♀, July, at light (U. K. Col. Lot 66, 73, 82) - 1♂, 2♀♀, September, at light (U. K. Col. Lot 115) - 1♂ (pale). MISSOURI, Lincoln Co., Clarksville, 22-VI-1953 about 200♀♀ and ♂♂; Taney Co., Hollister, 20-VII-1930 (H.H. Knight) - 10♀♀. WISCONSIN, Dane Co., 21-VI-1947, 24-VII-1947, and 27-VII-1947 - 3♀♀.

Note: All records are east of the 100th meridian except for a single specimen from New Mexico.

Hexagenia limbata (Serville) complex

Spieth's (1941) subspecies H. l. limbata, H. l. occulta, and H. l. venusta meet in a broad area of intergrades across Nebraska, Kansas, Iowa, northern Missouri, southern Minnesota, southern Wisconsin, Illinois, Indiana, and Ohio; H. l. occulta and H. l. viridescens intergrade in the Great Lakes region (Fig. 44). H. l. viridescens is not found in the area studied, and thus its synonymy, distribution, and records are not discussed. However, each subspecies is a quite distinct entity in its own region; typical H. l. limbata being found in the northwest, H. l. venusta in the south, H. l. occulta in the northeast, and H. l. viridescens just north of H. l. occulta. If these forms were not considered subspecies (Burks, 1953), the resulting H. limbata would consist of an

extremely variable population in the center of its geographical area, with different and distinct color phases in the northeast, south, and northwest. Since these populations at the geographical extremes of H. limbata are distinct and rather constant, the subspecific concept of Spieth (1941) is retained, although in the broad, central geographic area it is impossible to assign specimens to a particular subspecies.

Since the distributional information concerning the subspecies of this group is being added to, new subspecific records outside of the Missouri River watershed are included.

Hexagenia limbata limbata (Serville)

Ephemera limbata Serville, in Guérin Méneville, 1829, 384.
Palingenia limbata, Pictet, 1843, 146; Walker, 1853, 548; Hagen, 1861, 41; Walsh, 1862, 373; Hagen, 1863, 176; Provancher, 1876, 265.
Hexagenia limbata, Walsh, 1863, 197; Eaton, 1868, 85; Eaton, 1871, 65; Hagen, 1890, 11; Needham, 1920, 279; McDunnough, 1924b, 90; McDunnough, 1927, 119; Traver, 1931, 611 (in keys); Needham, Traver, and Hsu, 1935, 265; Burks, 1953, 39.
Hexagenia limbata limbata, Spieth, 1941, 246.
Hexagenia variabilis Eaton, 1883, 55 (in part).

The distribution and hybridization of H. l. limbata is shown in Fig. 44. The abdominal color pattern of H. l. limbata (Fig. 22) is intermediate between that of H. l. occulta (Fig. 23) and H. l. venusta (Fig. 24).

The nymph has not been described.

Recorded distribution of H. l. limbata; British Columbia, Colorado, Idaho, Illinois, Michigan, Oregon, Utah, and Washington.

Recorded distribution of hybrids: H. l. limbata x occulta - Illinois, Manitoba; H. l. limbata x venusta - Iowa, Kansas, Utah; H. l. limbata x occulta x venusta - Illinois.

New records of H. l. limbata: IOWA, Clayton Co., 13-VI-1932 (Russel) - 1♀, 12-VIII-1932 (M.W.J.) - 1♀; Dickinson Co., 28-VI-1935 (Gould Warren) - 1♀, 2-VII-1936 (P. Travis) - 2♂♂, 26-VII-1935 (R. Huizinga) - 1♂, 2-VIII-1938 (J.B.J.) - 1♀; Floyd Co., Charles City, 21-VIII-1918 (E.V. Walter) - 1♀; Franklin Co., Hampton, 17-VIII-1942 (W.W. Darlington) - 1♀; Henry Co., 19-V-1948 (Griffen) - 1♀, 12-VI-1951 (Herb Miller) - 1♀, 17-VI-1951 (Widmer) - 1♀, 27-VI-1947 (Toker) - 1♀, 13-VII-1948 (S. Statler) - 1 ♀ (subimago), 23-VII-1948 (S. Statler) - 1♀, 15-IX-1951 (Oppenheimer) - 1♀; Muscatine Co., 7-VI-1936 (Bernard Berger) - 1♀; Story Co., Ames, 29-III-1949 (Shoenhair) - 1♀, 28-V-1933 (Ruth Madden) - 1♀, no data - 1♂, 7-VI-1925 and 9-VI-1925 (C. W.M.) - 3♀♀, 18-VII-1946 (J. Laffoon) - 1♀, Gilbert, 16-VI-1928 (G. Hendrickson) - 1♀. KANSAS, Douglas Co., 14-VI-1921 (W.J. Brown) - 1♀. MICHIGAN, Ingham Co., East Lansing, 28-VI-1899, Lot 138, Sub. 10 - 3♀♀; 15-VI-1898 - 1♂, 26-VII-1890 - 1♂, 20-VII-1897 - 1♀, 25-VI-1895 - 1♀, all in Lot 129, Sub. 41 (det. by Nathan Banks), Aurelius, 10-VII-1938 - 5♀♀. MINNESOTA, Crow Wing Co., Nisswa, Pelican Lake, 12-VII-1912 (L. Bruner) - 1♀; Stearns Co., Sauk Center, 7-VIII-1954, at light (E.W. Hamilton) - 2♀♀. NEBRASKA, Buffalo Co., Kearney, 13-VI-1952, at light (E.W. Hamilton) - 1♂; Keith Co.,

Ogallala, 2-VII-1954, at light (E.W. Hamilton) - 1♀; Madison Co., Norfolk, 14-VII-1949, at light (M.H. Muma) - 1♂; Platte Co., Columbus, 26-VI-1950, on stream surface (E.W. Hamilton) - 1♀; Scotts Bluff Co., Mitchell, 14-VII-1915 (L.M. Gates) - 1♂. WISCONSIN, Dane Co., 17-VI-1946 and 13-VII-1946 (J.R.D.) - 2♀♀, 15-VIII-1947 - 1♀.

New records of H. l. limbata x occulta: IOWA, Clay Co., 5-VI-1933 (Maurer) - 1♂; Clayton Co., 3-VIII-1932 (M.W.J.) - 1♂, 9-VIII-1932 (Cronn) - 1♂ subimago; Dickinson Co., 19-VI-1936 (D. Millspaugh) - 1♂, 3-VII-1936, 9-VII-1936, 28-VII-1936, and 9-VII-1937 (H.E. Jaques) - 4♂♂, 13-VII-1936 (M.E. Barres) - 1♂; Henry Co., 9-VII-1947 (Swanson) - 1♀. MINNESOTA, Crow Wing Co., Nisswa, Pelican Lake, 12-VII-1912 (L. Bruner) - 2♂♂. 1♀. WISCONSIN, Dane Co., 16-VIII-1947 - 1♀.

New records of H. l. limbata x venusta: IOWA, Davis Co., Floris, 9-VIII-1941 (Calhoun) - 1♀; Dickinson Co., 23-VI-1934 (W.E. Dodds) - 1♀, 28-VI-1935 and 5-VII-1935 (Mabel Jaques) - 2♀♀, 2-VII-1935 and 5-VIII-1935 (H. Huizinga) - 1♂, 1♀, 3-VII-1936, 13-VII-1936, 2-VIII-1937, and 8-VIII-1935 (H.E. Jaques) - 3♀♀, 1♀ subimago, 2-VII-1934 (H.C. Knutson) - 1♂ subimago, 7-VII-1937 (George Crane) - 1♂; Henry Co., 20-VII-1937 (Donovan Orman) - 1♂ subimago, 28-VI-1951 (Benjamin Luke) - 1♀, Mt. Pleasant, 29-VII-1942 (L. Wright) - 1♀ subimago, 5-VIII-1942 (A. Pidgeon) - 1♀ subimago; Story Co., 28-V-1941 (L. Polter) - 1♀, 4-VI-1949 (Totemeier) - 1♂, 12-VI-1953 and 19-VI-1953 (W.S. Craig)- 1♂, 2♀♀, 1♂ subimago, 9-VII-1948 (W. Luginbuhl) - 1♀ subimago, NEBRASKA, Brown Co., Johnstown, 4-VIII-1950, Plum Creek (E.G. Burcham) - 1♀; Buffalo Co., Kearney, 13-VI-1952, at light (L.W. Quate) - 1♀; Cherry Co., Valentine, 30-VIII-1954, at light (E.W. Hamilton)- 1♂, 2♀♀, 30-VIII-1954, at light (L.W. Quate) - 1♂, 1♀; Dawson Co., Lexington, 28-VI-1950, at light (O.S. Bare) - 6♂♂, Willow Island, 15-VII-1954, on potatoes (R.E. Hill) - 1♂; Douglas Co., Omaha, 5-VIII-1913 and 12-VIII-1913 (L.T. Williams)- 1♂, 1♂ subimago; Keith Co., Ogallala, 2-VIII-1954 and 10-VIII-1955, at light (E.W. Hamilton)- 1♀, 1♂ subimago; Lincoln Co., North Platte, 30-VII-1949, at light (E.W. Hamilton) - 1♀; Madison Co., Norfolk, 25-VI-1913 (L.T. Williams) - 1♂, 1♀, 15-VI-1949, at light (D. Scott) - 5♂♂ subimagoes, 16-VI-1949, at light (M.H. Muma) - 1♂, 30-VI-1949, at light (M.H. Muma)- 2♂♂, 3♀♀, 14-VII-1949, at light (M.H. Muma)- 1♀; 5-VIII-1949, at light (M.H. Muma) - 1♂; Platte Co., Columbus 2-VII-1950, at light (E.W. Hamilton) - 1♂; Scotts Bluff Co., Scottsbluff, 10-VI-1952, at light (E.W. Hamilton) - 1♂, 26-VIII-1949, at light (J. Weimer) - 1♀; Thomas Co., Halsey, 13-VIII-1912 (J.T. Zimmer) - 1♂. NORTH DAKOTA, Cass Co., 4-VII-1930 (Adrian Fox) - 1♀, 21-VI-1941, 4-VII-1941, at light (H.S. Telford) - 1♂, 1♀, no date - 3♀♀. WYOMING, Goshen Co., Torrington, 27-VIII-1947 and 2-IX-1948 (R.E. Pfadt) - 3♂♂, 2♀♀.

Hexagenia limbata occulta (Walker)

Palingenia occulta Walker, 1853, 551.
Hexagenia limbata var. occulta, McDunnough, 1927, 119.
Hexagenia occulta, Traver, 1931, 611 (in key); Needham, Traver, and Hsu, 1935, 267.
Hexagenia limbata occulta, Neave, 1932a, 182; Neave, 1932b, 54; Spieth, 1940, 327; Spieth, 1941, 250.
Hexagenia variabilis (in part) Eaton, 1883, 55; Hagen, 1890, 12; Needham, 1901, 427; Needham, 1908, 262; Morgan, 1911, 99.
Hexagenia mingo Traver, 1931, 597; Needham, Traver, and Hsu, 1935, 267. (synonymy after Spieth, 1941)
Hexagenia rosacea Traver, 1931, 607; Needham, Traver, and Hsu, 1935, 273. (synonymy after Spieth, 1941)

Spieth in his discussion of the North American species of Francis Walker (1940, p. 332) writes, "A careful study of the eye size, the remaining abdominal color pattern and the coloration of the head, cerci and wings indicates that (Baetis) angulata Walker is a synonym of H. viridescens Walker instead of H. bilineata Say as indicated by Eaton, or H. l. occulta Walker as McDunnough and Traver have held." Since Spieth (1941) in his revision did not include B. angulata Walker in the synonymy of H. viridescens, it is mentioned here to clarify its standing.

The distribution and hybridization of H. l. occulta is shown in Fig. 44. Dark specimens of H. l. occulta are practically indistinguishable from H. viridescens, a subspecies of the Great Lakes region. One must be careful also not to confuse H. l. occulta (Figs. 15, 23) with H. bilineata (Figs. 19, 21) as has often been done.

The nymph has been described by Neave (1932) and Spieth (1941).

Recorded distribution of H. l. occulta: District of Mackenzie, Illinois, Indiana, Kentucky, Manitoba, Michigan, Minnesota, New Brunswick, New York, North Carolina, North Dakota, Ohio, Ontario, Province of Quebec, Saskatchewan, West Virginia, and Wisconsin.

Recorded distribution of hybrids: H. l. limbata x occulta - Illinois, Manitoba; H. l. limbata x occulta x venusta - Illinois; H. l. occulta x venusta - Illinois, Indiana, Manitoba, Minnesota, Ohio.

New records of H. l. occulta: IOWA, Clayton Co., 10-VI-1938 (Harold Beery) - 3♂♂; Dickinson Co., 19-VI-1936 and 30-VII-1937 (H. E. Jaques) - 1♂, 1♀, 19-VI-1936 (D. Millspaugh) - 1♂; Henry Co., 17-VI-1951 (Widmer) - 1♂; Lee Co., 21-V-1949 (Ivor Koch) - 1♂ subimago; Linn Co., 19-VI-1934 (H.C. Knutson) - 1♂; Lyon Co., 27-VI-1940 (H.E. Jaques) - 1♂, Beloit, 27-VII-1928 (G. Hendrickson) - 1♂; Plymouth Co., 2-VIII-1921 (L.S.) - 1♂; Story Co., Ames, ?-V-1940 (Ellis Hicks)-1♂ (very purplish), 4-VII-1946 (J. Laffoon) - 1♂ (# 701), 30-V-1949 (Shoenhair) - 1♂. MANITOBA, Hartney, 31-VII-1937 (C. L. Johnson) - 1♂. MICHIGAN, Bay Co., Bay City, 28-VI-1899 - 21♂♂, 2♀♀; Cheboygan Co., Douglas Lake, ?-VI-1927 (Leonora K. Gloyd) - 2♂♂ subimagoes. MINNESOTA, Crow Wing Co., Nisswa, Pelican Lake, 12-VII-1912 (L. Bruner) - 8♂♂, 2♀♀, 3♂♂ subimagoes. NORTH DAKOTA, Cass Co., Fargo, no other data - 4♂♂, 1♀.

WISCONSIN, Dane Co., 3-VIII-1946 (J.R.D.) - 1♂, 8-VIII-1947 - 2♂♂; Vilas Co., Eagle River, 3-VII-1952, at light (H.J. Ball) - 3♂♂, 3♀♀.

New records of H. l. occulta x venusta: IOWA, Davis Co., Floris, 9-VIII-1941, (Calhoun) - 2♂♂; Dickinson Co., 23-VI-1934 (W.E. Dodds) - 1♂, 5-VII-1935, 3-VII-1936, 13-VII-1936, and 27-VII-1936 (H. E. Jaques) - 4♂♂; Emmet Co., 24-VII-1932 (Iles) - 1♂; Muscatine Co., Muscatine, 23-VI-1953, at light (W.S. Craig) - 1♂, 1♀; Story Co., Ames, ?-V-1940 (Ellis Hicks) - 1♂, 23-V-1941 (Levi Mohler) - 1♀, 30-VI-1948 (R.E. Nelson) - 1♀. NEBRASKA, Platte Co., Columbus, 2-VII-1950, reared from swift stream (E.W. Hamilton) - 1♂. WISCONSIN, Dane Co., 3-VIII-1947 - 1♂.

Hexagenia limbata venusta Eaton

Hexagenia venusta Eaton, 1883, 54; Ulmer, 1921, 235, 237, 239; McDunnough, 1927, 119 (in discussion of H. affiliata); Traver, 1931, 611 (in key); Needham, Traver, and Hsu, 1935, 274; Spieth, 1941, 88.

Hexagenia limbata venusta, Spieth, 1941, 253.

Hexagenia pallens Traver, 1935, (in Needham, Traver, and Hsu) 271 (synonymy after Spieth, 1941).

The distribution and hybridization of H. l. venusta is shown in Fig. 44, its abdominal color pattern in Fig. 24.

The nymph has been described by Spieth (1941).

Recorded distribution of H. l. venusta: Illinois, Iowa, Kansas, Mississippi, Missouri, Nebraska, Oklahoma, Tennessee, and Texas.

Recorded distribution of hybrids: see H. l. limbata and H. l. occulta.

New records of H. l. venusta: IOWA, Dickinson Co., 29-VI-1934 (H.C. Knutson), 28-VI-1935 (Gould Warren), 9-VII-1937, 2-VIII-1937, and 8-VIII-1935 (H.E. Jaques) - 3♂♂ (1 subimago), 2♀♀; Henry Co., 20-VII-1951 (Miller) - 1♀, 25-VII-1951 (Ginkens) - 1♀; Iowa Co., Lake Amana, 23-VI-1928 (G.O. Hendrickson) - 1♂; Story Co., Ames, 4-VI-1930 (H.E.G.), 1-VIII-1939 (E. Buren), no date (Osborn) - 2♂♂, 1♀. KANSAS, Douglas Co., Lawrence, ?-VI-? (H.T. Martin) - 1♂ (#7 determined by N. Banks), ?-VII-? (U. of K. Col. Lot 66 and 71) - 2♀♀. ?-VII-? (U. of K. Col. Lot 97) - 1♀ (all taken at lights); Ellis Co., 14-VII-1912, 2000' (F.X. Williams) - 1♂; Franklin Co., 1-VII-1912 (H.K. Gloyd) - 2♀♀; Gove Co., no date, 2813' (F.X. Williams) - 1♀ subimago; Graham Co., 16-VIII-1912, 2130' (F.X. Williams) - 2♂♂; Greenwood Co., 31-VII-1923 (Beamer - Lawson) - 3♀♀; Pratt Co., 6-VI-1950 (J.G. Rozen) - 1♀ subimago; Reno Co., 21-VII-1947 - 7♀♀, 21-IX-1949 - 1♀; Riley Co., Manhattan, 6-VI-1949, at light (R.L. Fischer) - 6♀♀, 10-VI-1942, on alfalfa (Roger C. Smith) - 1♂, 1♀, ?-VII-1929 (T.F. Winburn) - 1♀, 2-VII-1941, on alfalfa (Roger C. Smith) - 1♀; Rooks Co., 9-VIII-1912, 1775' (F.X. Williams) - 1♂, 1♀; Scott Co., 20-VI-1925 (H.O. Deay) - 1♀. MICHIGAN, Ingham Co., East Lansing, 8-VI-1900 - 12♀♀, 7-VI-1899 and 18-VI-1899 - 4♀♀. MISSOURI, Boone Co., Columbia, 28-VI-1953, at light (W.R. Enns) - 3♀♀, 2♀♀ subimagoes; Pike Co., Louisiana, 15-VI-1953 (W.R. Enns) - 2♂♂, 2♀♀ (all subimagoes), Clarksville, 15-VI-1953, at light (W.R.

Enns) - 3♀♀. NEBRASKA, Buffalo Co., Kearney, 13-VI-1952 (L.W. Quate) - 1♀; Dawson Co., Johnson Lake, 25-VIII-1955, at light (O.S. Bare) - 1♂ subimago, Lexington, 28-VI-1950, at light (O.S. Bare) - 4♀♀, 7-VII-1955, on potatoes (R.E. Hill) - 1♂; Douglas Co., Omaha, 12-VII-1913 and 5-VIII-1913 (L.T. Williams) - 2♂♂, 2♀♀; Keith Co., Ogallala, 2-VIII-1954, at light (E.W. Hamilton) - 2♀♀, 19-VII-1955, at light (D. Scott) - 2♂♂ subimagoes; Lancaster Co., Lincoln, 20-X-1949, in pond (E.W. Hamilton) - 2 nymphs, 3-VII-1950, at light (E.W. Hamilton) - 1♂; Lincoln Co., North Platte, 11-VII-1955, at light (E. W. Hamilton) - 3♂♂; Madison Co., Norfolk, 16-VII-1949, at light (M. H. Muma) - 1♀; Platte Co., Columbus, 26-VI-1950 and 2-VII-1950, at light (E.W. Hamilton) - 1♂, 1♀; Scotts Bluff Co., Scottsbluff, 10-VI-1952, at light (E.W. Hamilton) - 1♀; Seward Co., Milford, 3-VII-1954, at light (E.W. Hamilton) - 1♀, Seward, 15-VIII-1949, at light (E.W. Hamilton) - 1♂, 5 ♀♀ subimagoes, 26-VI-1950, at light (E.W. Hamilton) - 1♀. TEXAS, Eastland Co., Cisco, 19-VI-1947 (A.C. Michener) - 6♀♀, Wiley, 2-IX-1920 (Grace Olive) - 1♀.

Hexagenia munda Eaton complex

This species has not been found in the Missouri River watershed, but is reported from Iowa and Missouri in the Mississippi drainage. The complex is distinguishable from H. limbata (Serville) only by very slight genitalic differences (Fig. 17) and by a uniform umber pigmentation of the costal membrane with the costal cross-veins not margined.

Hexagenia munda affiliata McDunnough

Hexagenia affiliata McDunnough, 1927, 118; Traver, 1931, 611 (in key); Needham, Traver, and Hsu, 1935, 261.
Hexagenia munda affiliata, Spieth, 1941, 257.

This subspecies is very close to H. l. occulta in its dorsal abdominal maculations (Fig. 25a). It can be distinguished from H. l. occulta and other species by its costal pigmentation, penes (Fig. 16), and abdominal pattern (Fig. 25).

The nymph is undescribed.

Recorded distribution: Connecticut, Indiana, Iowa, Maine, Michigan, Minnesota, New Hampshire, New Jersey, New York, Ohio, Ontario, Pennsylvania, and Quebec.

New records: IOWA, Delaware Co., 10-VI-1932 (Moore) - 1♂; Linn Co., 19-VI-1934 (H.C. Knutson) - 1♂.

Note: All records are east of the 100th meridian.

Hexagenia munda munda Eaton

Hexagenia munda Eaton, 1883, 53; McDunnough, 1927, 118; Needham, Traver, and Hsu, 1935, 268; Burks, 1953, 41.
Hexagenia munda munda, Spieth, 1941, 263.

The nymph has not been described.

Recorded distribution: Illinois, Missouri, Oklahoma.
Note: All records are east of the 100th meridian.

Hexagenia rigida McDunnough

Hexagenia rigida McDunnough, 1924b, 90; McDunnough, 1927, 117 (in discussion); Traver, 1931, 611 (in key); Neave, 1932a, 1; Neave, 1932b, 54; Needham, Traver, and Hsu, 1935, 272; Spieth, 1941, 267; Burks, 1953, 41.

This is another species that can be confused with H. l. occulta, particularly the females. Quite often the ventral abdominal markings (Fig. 27b) become obscured by dark pigmentation, the pattern thus looking more like that of H. l. occulta (Fig. 23b). Some light specimens of H. l. occulta have the ventral abdominal pattern approaching that of H. rigida. However, the eggs of the two species (Neave, 1932), the nymphs, and the male genitalia are quite different.

The nymph has been described by Neave (1932) and Spieth (1941).

Recorded distribution: Illinois, Iowa, Kansas, Manitoba, Michigan, Missouri, New Brunswick, New York, Ohio, Oklahoma, Ontario, Pennsylvania, Quebec, and Vermont.
Note: All records are east of the 100th meridian.

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PLATE I

Figure	Species	Character
1	Heptagenia elegantula	Wings
2	Isonychia sicca	"
3	Tortopus primus	"
4	Ephoron album	"
5	Potamanthus verticis	"
6	Ephemera simulans	"
7	Pentagenia vittigera	"
8	Hexagenia bilineata	"
9	Diagram showing wing fluting	

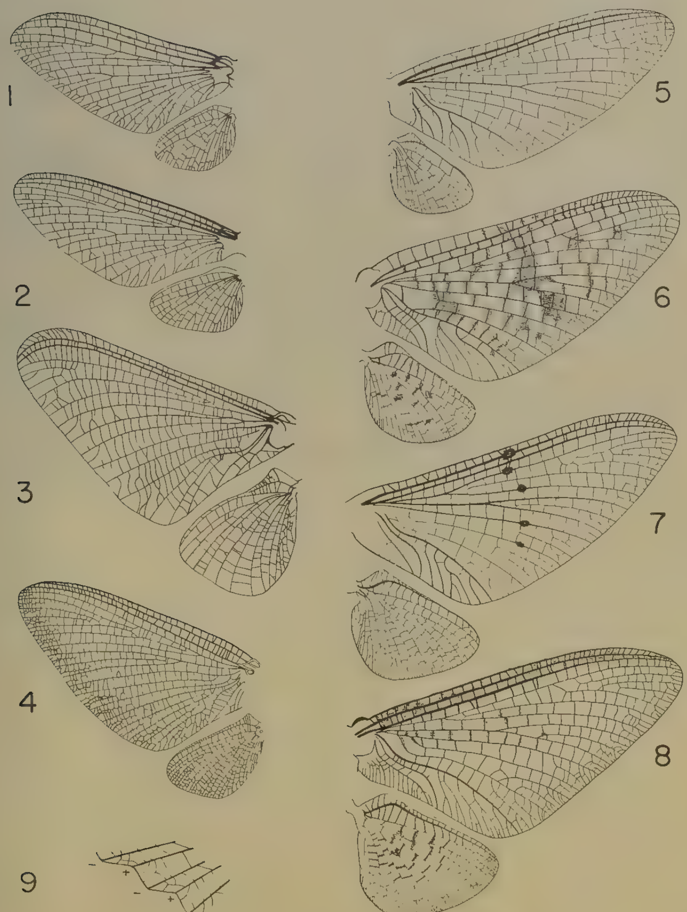
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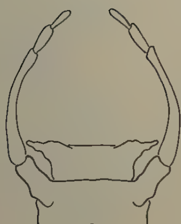
PLATE II

Figure	Species	Character
10	Ephoron album	Penes
11	Potamanthus rufus	"
12	Pentagenia vittigera	"
13	Ephemera simulans	"
14	Hexagenia atrocaudata	"
15	Hexagenia limbata limbata	"
16	Hexagenia munda	"
17	Hexagenia rigida	"
18	Tortopus primus	"
19	Hexagenia bilineata	"



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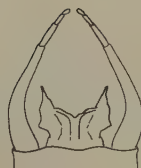

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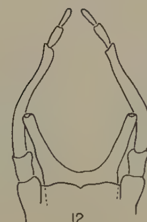

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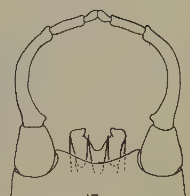

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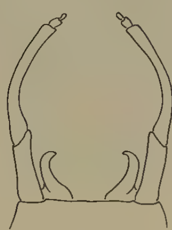

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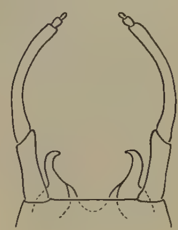

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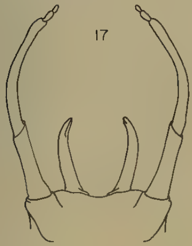

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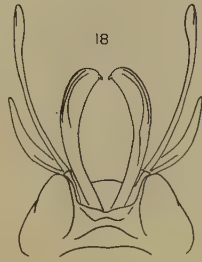

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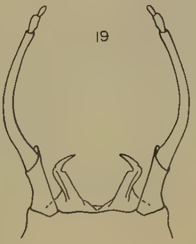

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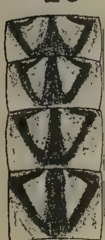
PLATE III

Figure	Species	Character
20	Hexagenia atrocaudata	Abdominal terga 3-6
21a	Hexagenia bilineata	" " 3-6
b		" sterna 3-6
22a	Hexagenia limbata limbata	" terga 3-6
b		" sterna 3-6
23a	Hexagenia limbata occulta	" terga 3-6
b		" sterna 3-6
24a	Hexagenia limbata venusta	" terga 3-6
b		" sterna 3-6
25a	Hexagenia munda affiliata	" terga 3-6
b		" sterna 3-6
26a	Hexagenia munda munda	" terga 3-6
b		" sterna 3-6
27a	Hexagenia rigida	" terga 3-6
b		" sterna 3-6
28	Pentagenia vittigera	" terga 3-6



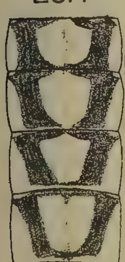
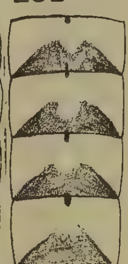


20 21A 21B 22A 22B






23A 23B 24A 24B 25A 25B


26A 26B 27A 27B 28

PLATE IV

Figure	Species	Character
29	Potamanthus sp.	Whole nymph
30	Hexagenia limbata	" "
31	Ephoron album	Nymph head and tusks
32	Pentagenia vittigera	" " " "
33	Ephemera simulans	" " " "
34	Hexagenia atrocaudata	" " " "
35	Hexagenia bilineata	" " " "
36	Hexagenia munda	" " " "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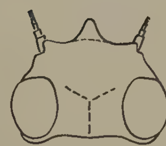
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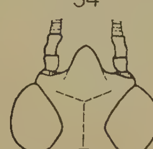
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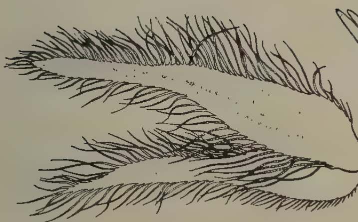
PLATE V

Figure	Species	Character
37	*Hexagenia limbata*	Nymph gills on 1-4
38	*Ephoron leukon*	" " " "
39	*Potamanthus myops*	" " " "
40	*Pentagenia vittigera*	" " " "
41	*Hexagenia bilineata*	Nymph mid-tarsal claw
42	*Hexagenia munda*	" " "
43	*Hexagenia rigida*	" " "



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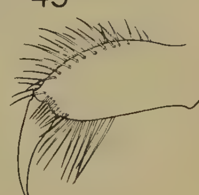

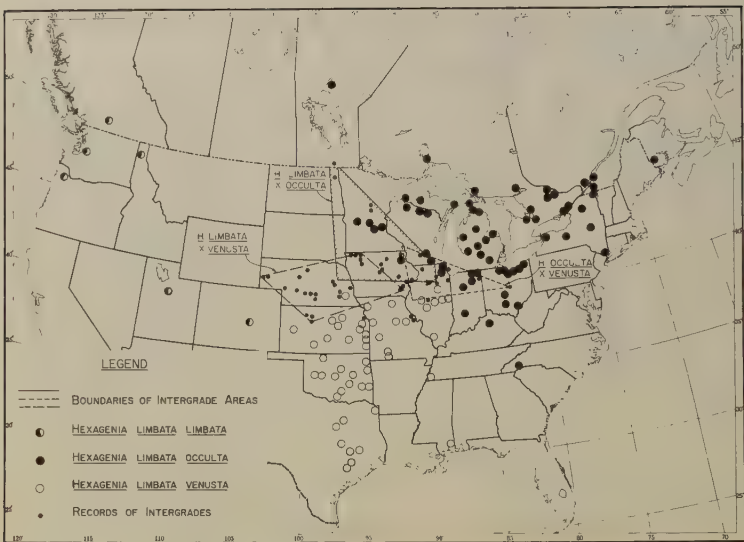

PLATE VI

Fig. 44. Hexagenia limbata. Distribution map of subspecies and apparent areas of intergradation.

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RESPONSES OF ROSE PLANTS TO CANE COATING WITH MELTED PARAFFIN WAX[1]

S.J. Toy[2] and J.P. Mahlstede[3]

Although coating of the canes of dormant rose plants by dipping in melted paraffin wax has been a nursery practice for more than twenty-five years, few critical studies on the effects of the process have been made. There are also differences of opinion as to the value of waxing, among both nurserymen and gardeners.

The process of waxing appears to have developed somewhat empirically, based mostly on observations and small trials (7, 8, 17). A series of articles by Neilson(9, 10, 11, 12, 13) probably gave the greatest impetus to the adoption of the procedure by nurserymen, although little experimental data were then available. Tukey and Brase (14) studied the effects of various storage treatments on sweet cherry trees and roses. They found that waxing was beneficial to the roses but not to the cherry trees. Moore (6) found that waxing roses offered some protection against winter-killing. Foret (1) compared waxed and untreated roses in a field test but found no differences. Johnson and Janne (3) reported on some field tests of waxed and unwaxed roses and concluded that the waxed roses started growth sooner, bloomed earlier and more profusely, and were more vigorous. Lyle (4) studied the effect of waxing temperatures on roses and found no apparent injury even at 208 °F and a dipping time of six seconds.

MATERIALS AND METHODS

Three experiments were carried out to study various aspects of rose waxing: 1) a field experiment; 2) a controlled humidity storage experiment; and 3) a laboratory desiccation experiment.

The field experiment was carried out from the spring of 1957 through the spring of 1958. Two hundred seventy, number one grade, hybrid tea rose plants, variety Crimson Glory, were divided into three groups of 90 plants each for planting on April 29, May 27, and June 24. Each planting was in turn divided into 3 groups of 30 plants each for treatment. One group was waxed with cream rosebush wax[4], the second group with light green rosebush wax from the same source, and the third group was left unwaxed as the control. All plants were top pruned to 16 inches,

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[3]Professor of Horticulture, Horticulture Department.

[4]National Wax Company, Chicago, Illinois.

root pruned to 10 inches, and root wrapped with sphagnum moss and moistureproof paper before waxing. Waxing temperatures were between 188 and 191°F. After waxing, all plants were placed in cold storage for two weeks followed by one week at higher temperatures in a frame shed to simulate shipping and handling. The field planting was arranged as a randomized block design with 6 blocks. Data were taken on the basis of 5 plants per experimental unit.

The controlled humidity storage experiment was carried out in the spring and summer of 1958 using a walk-in type refrigerator into which were placed three old household type refrigerator cabinets for humidity controlled spaces. The relative humidities maintained were approximately 50, 75, and 100 per cent. This was accomplished by placing a pan of saturated salt solution in each cabinet, over which circulation of air was maintained by a two-inch diameter fan. For the 50 and 75 per cent relative humidities the salts used were sodium bisulfate (2) and sodium chloride (16) respectively. For the 100 per cent relative humidity, the pan was filled only with distilled water. The temperature was maintained at 45°F throughout the experiment except during the second and third weeks when it was raised to 65°F to permit some shoot and root growth. Ninety plants were used in the experiment, divided into 3 groups of 30 plants each for treatment. One group was waxed with "cream" wax, another group was dipped in hot water the same temperature as the wax, and the remaining group was left untreated for comparison. The treatments were each further divided into 3 groups of 10 plants for storage at each of the 3 different humidities. The purpose of the hot water treatment was to test the effect of waxing temperatures alone, without actually having wax on the canes.

The desiccation experiment consisted of cutting stem sections into three-inch lengths, applying the treatments, and placing on a glass plate in the laboratory to permit evaporation of moisture. For comparison with roses, stem sections of althea (_Hibiscus syriacus_) and privet (_Ligustrum amurense_) were also used. Treatments were: completely waxed, ends only waxed, and no treatment. Specimens were weighed before treatment and per cent weight loss was based on the original untreated weight. Weighings were made daily for the first few days and the interval increased to 2 and 3 days after the rate of weight loss decreased. Five replicates were used for each treatment. Temperatures during the 23 days of the experiment varied between 68.0 and 78.5°F and relative humidities ranged between 38 and 74 per cent.

RESULTS

Field Experiment

Measurements taken were 1) dates of flowering and number of flowers, 2) per cent of original cane length surviving, 3) number of new shoots, 4) total length of new growth, 5) weight of roots, 6) number of new roots, 7) number of plants surviving over winter, and 8) number of flowers the second spring.

Table 1 is a summary of all measurement data, giving the mean values

Table I. Statistical summary of field experiment

	Date Means			Wax Means			Statistical Differences				
	Apr. 29	May 27	June 24	Cream wax	Green wax	Un-waxed	Between planting dates	Between waxes	Cream wax vs. green wax	Cream + green wax vs. unwaxed	Interaction, dates x waxes
Flowers per plant 1957	42.9	23.0	7.6	27.7	28.4	17.4	**	**	ns	**	**
% original cane length surviving	68.0	60.0	58.0	74.6	75.7	35.1	**	**	ns	**	**
No. of new shoots per plant	18.3	14.7	12.0	17.3	17.8	9.9	**	**	ns	**	**
Total shoot growth per plant (inches)	180	113	66	138	141	81	**	**	ns	**	**
Root weight per plant (grams)	110	93	76	99	98	82	**	**	ns	**	ns
No. of new roots per plant	29.8	20.1	15.9	24.6	24.5	16.8	**	**	ns	**	**
No. of plants per 5 surviving over Winter	4.50	3.94	2.44	3.83	4.00	3.06	**	**	ns	**	ns
Flowers per plant 1958	11.9	5.8	5.4	9.96	8.48	4.67	*	ns	ns	*	ns

* Significant at 5% level
** Significant at 1% level
ns No significant difference

for the various factors. There was no significant difference between the cream wax and the green wax in any of the eight measurements taken. On the other hand, differences were statistically significant between the waxed plants and the unwaxed plants in all measurements.

It is noted that in some measurements there is a significant interaction between date of planting and wax treatment. This is because the differences between waxed and unwaxed in the third planting are not in the same proportion as the differences in the first and second plantings. This can be explained by the fact that the weather the first few days after the third planting was made was relatively cool and humid, permitting the unwaxed plants to recover almost as rapidly as those protected by wax.

Weather data for the first five days after planting are given in Table 2. Note that immediately following the third planting, rainfall was more frequent, evaporation was less, wind movement was less, and temperatures were no higher than after the second planting. The weather data are from Climatological Data (15), from measurements originally made on the Iowa State College Agronomy Farm, less than one mile from the experimental plot.

The flowers were counted every three days, with a few exceptions, throughout the summer and fall. Each flower was counted and cut off the plant when its petals began to fall. Figure 1 shows the distribution of flower production based on data totaled at six-day intervals. For the first and second plantings, the first peak in flower production was delayed in the unwaxed plants compared with the waxed plants, although the second peak in flowering appears to coincide for all treatments. There was no corresponding difference in the third planting owing to the absence of the first peak resulting from the late planting date. Table 1 shows that, on the whole, the waxed plants produced about 65 per cent more flowers than the unwaxed plants.

The percentage of original cane length surviving was determined by measuring, at the end of the growing season, the total length of cane that had died, comparing this with the total original cane length of each plant. Table 1 shows that cane length survival was actually greater in the unwaxed plants of the third planting than the corresponding treatment of the second planting. This is due to the cool, humid weather following the third planting as shown in Table 2. On the whole, however, more than twice the original canelength of the waxed plants survived compared with the unwaxed plants.

The number of new shoots tended to show differences similar to percentage of original cane length survival. This is related to the length of cane remaining alive, from which the new shoots could arise. There were almost twice as many new shoots produced by the waxed plants as the unwaxed.

Total shoot growth was measured at the end of the growing season. Each shoot was individually measured and recorded, and when totaled, these data also yielded the number of new shoots per plant. Table 1 shows the waxed plants produced about 75 per cent more shoot length than the unwaxed plants.

Root data were collected early the second spring from four of the original six replicates. Two replicates were permitted to remain in the

Table 2. Weather for five days after each planting

Planting date	Day after planting 1st	2nd	3rd	4th	5th	Average
			Rainfall in inches			
April 29	0	0	0	Trace	0	Trace
May 27	0	.02	1.23	.01	0	0.25
June 24	.34	.03	.09	.08	0	0.11
			Evaporation in inches			
April 29	.25	.24	.27	.34	.25	.27
May 27	.27	.24	.25	.10	.33	.24
June 24	.13	.18	.10	.21	.24	.17
			Wind in miles per day			
April 29	36	31	72	126	77	68
May 27	83	81	55	20	99	68
June 24	66	38	34	47	33	44
			Average temperature in °F			
April 29	62	64	65	57	47	59
May 27	62	69	69	68	65	67
June 24	64	67	61	68	73	67

field for further observation. Root weights were taken of the entire root system below the bud union, after all soil was thoroughly shaken off. Root number included only the new roots that were one-sixteenth inch or larger in diameter. As shown in Table 1, differences between treatments were smaller than data taken on the tops, but these differences were nevertheless statistically significant. Root weight was about 20 per cent greater and the number of new roots was about 50 per cent greater in the waxed plants than in the unwaxed plants.

The number of plants surviving over winter was determined from all six replicates. Plants that were dug for root examination were counted as surviving if any live scion wood remained, and those that remained in the field were counted when growth resumed the second spring. As shown in Table 1, a greater percentage of the waxed plants survived, and the plants that were planted the earliest had the highest survival. Differences were small but highly significant. About 30 per cent more of the waxed plants survived compared with the unwaxed.

Flower production the second spring was recorded, since it appeared that the waxed plants were more vigorous. Data were taken only from the two replicates that remained in the field. Table 1 shows that the waxed plants produced about twice as many flowers as the unwaxed plants.

Data were taken only until July 12, as this appeared to be the end of the first flush of spring bloom. As little of the original waxed cane still remained at this time, the increased response of the waxed plants is undoubtedly due to the more vigorous growth of the entire plant the first year.

Figure 2 summarizes in graphic form the results of treatment by date combinations for all measurements. The differences between the waxed plants and the unwaxed plants are more readily visualized by this presentation. Notice that in some measurements the response of the waxed plants is more than twice that of the unwaxed plants. Also notice the reduced response due to delay in planting.

Controlled Humidity Storage Experiment

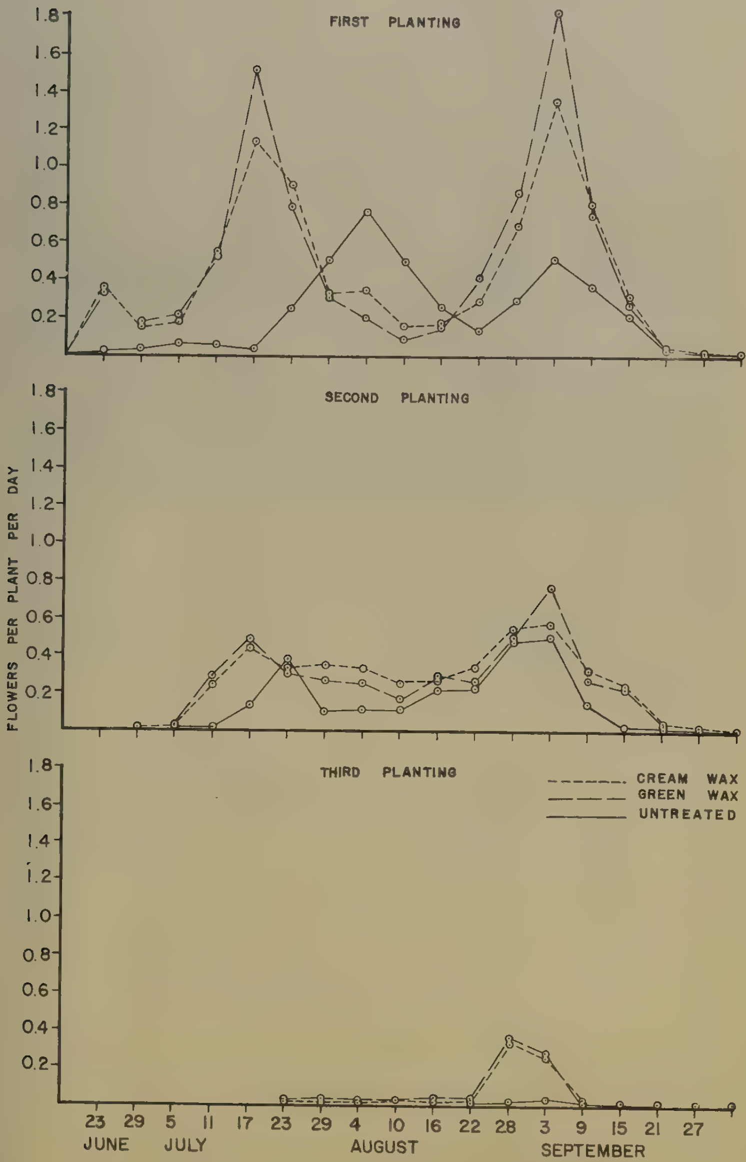
Measurements taken were: 1) shoot number, 2) shoot length, 3) mold growth, 4) percentage cane length dead, 5) root growth, and 6) cane moisture percentage.

Table 3 summarizes all measurement data and gives the mean values of the results of storage humidity and for treatments. In general, differences between treatments were highly significant in all measurements, although differences between storage humidities were not always significant.

Both shoot number and total shoot length per plant were determined by measuring and recording individually each shoot to the nearest centimeter. Only shoots one-half centimeter or longer were counted. Measurements were made four weeks after the experiment was started. Table 3 shows there were no significant differences due to storage humidity although the mean values show a trend toward lower response at lower humidity. There was, however, a great difference due to waxing, with the waxed plants producing about three times as many new shoots and about six times the new shoot length of the untreated.

Mold development on the canes and the percentage cane length dead were measured eight weeks after the experiment was started. Mold growth was evaluated by ranking each plant on a scale of one to four. One indicated no mold growth; 2, up to 10 per cent of the cane affected; 3, 10 to 20 per cent of cane affected; and 4, more than 20 per cent of the cane surface covered by molds. Table 3 shows there were highly significant differences due both to humidity and treatment. In general there was greater mold development at the higher humidities, with about 50 per cent more mold development at 100 per cent relative humidity compared with 50 per cent relative humidity. The waxed plants had only about 70 per cent as much mold as those left untreated.

Percentage cane length dead, like shoot number and shoot length, did not show significant differences due to humidity, although there was a trend toward more dead cane at the lower humidities. Differences between treatments, however, were highly significant. About 40 per cent more cane died in the untreated than in the waxed plants in spite of the fact that storage humidity had little effect. More than twice as much cane died in the hot water treated plants as the untreated, but this was due to direct injury to cane tissues by the hot water.


FIRST PLANTING
SECOND PLANTING
THIRD PLANTING
CREAM WAX
GREEN WAX
UNTREATED
FLOWERS PER PLANT PER DAY
1.8
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
23 29 5 11 17 23 29 4 10 16 22 28 3 9 15 21 27
JUNE JULY AUGUST SEPTEMBER

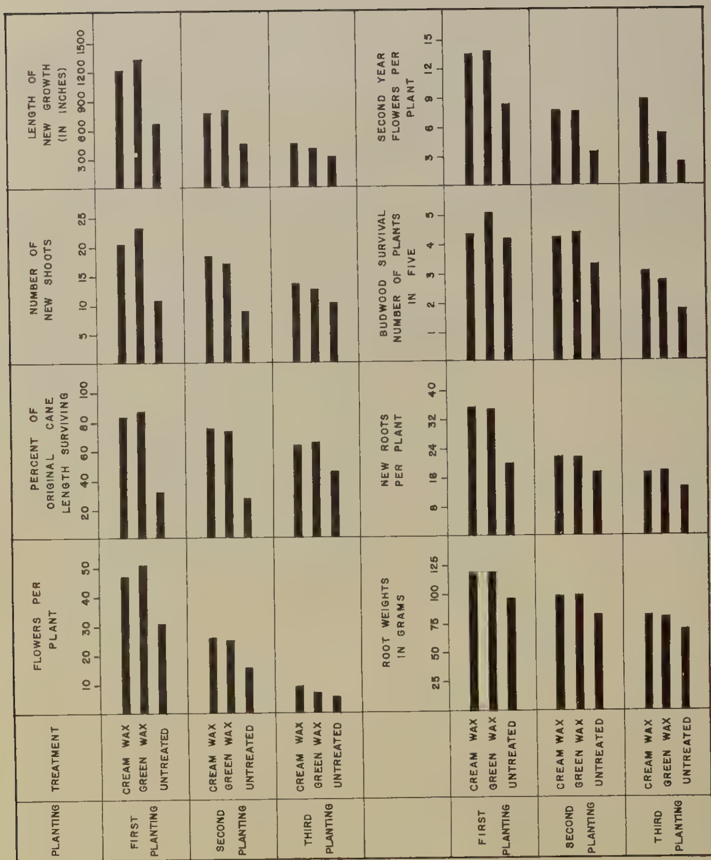


FIGURE 2. GRAPHIC SUMMARY OF FIELD EXPERIMENT

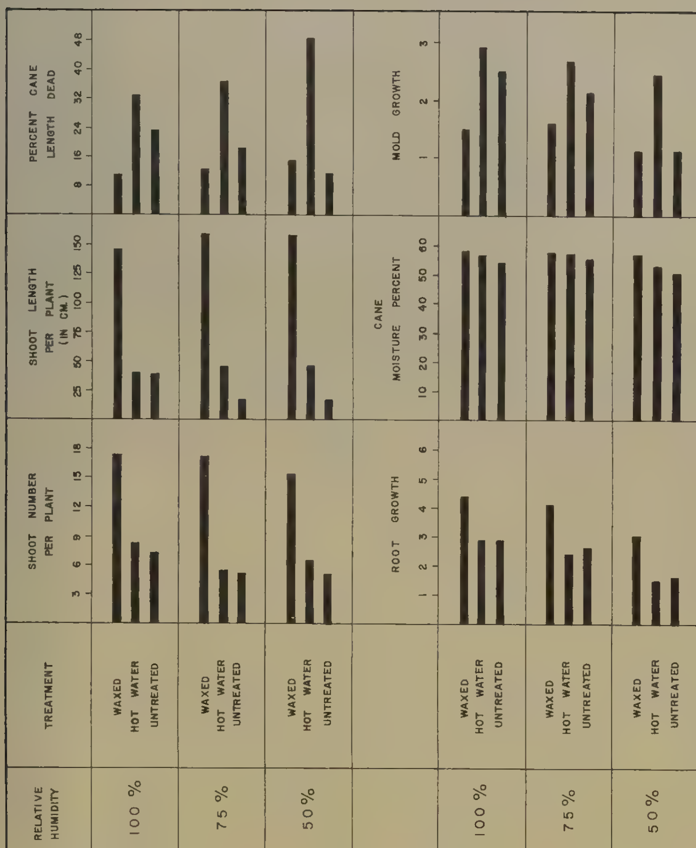


FIGURE 3. GRAPHIC SUMMARY OF CONTROLLED HUMIDITY STORAGE EXPERIMENT

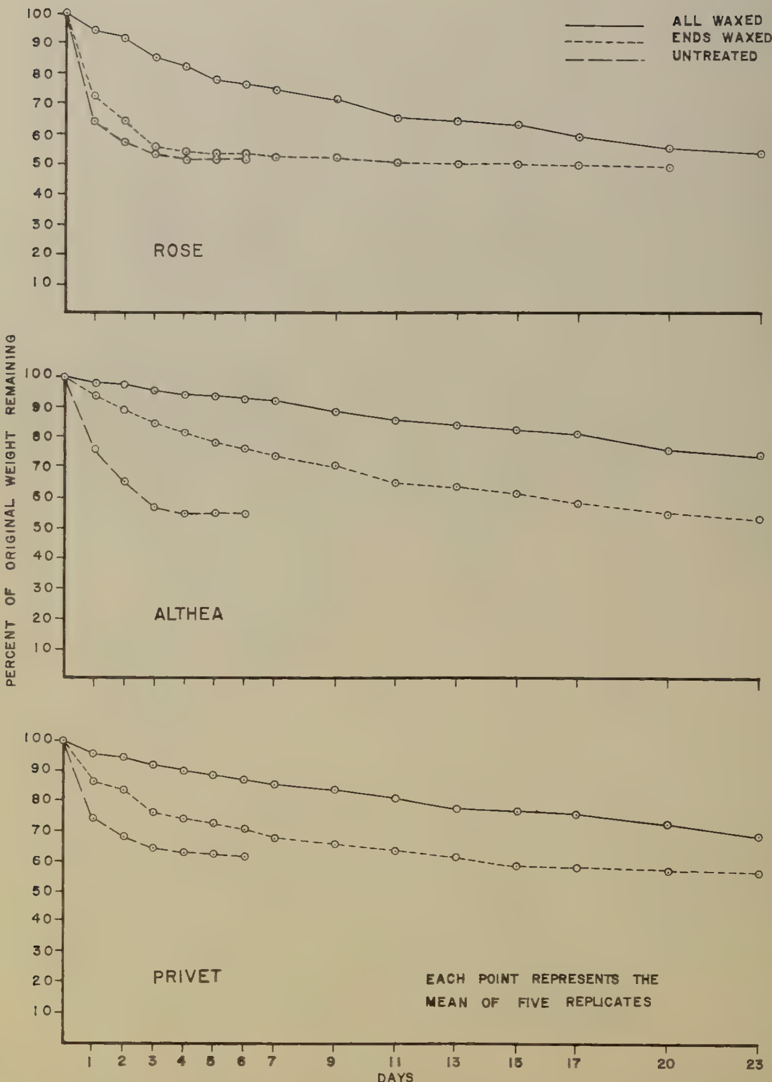


FIGURE 4. LOSS IN WEIGHT OF TREATED STEM SECTIONS

Table 3. Statistical summary of controlled humidity storage experiment

	Humidities			Treatments			Statistical Differences		
	100%	75%	50%	Waxed	Hot water	Un-treated	Between humidities	Between treat-ments	Interaction, treatments x humidities
Shoot No. per plant	11.1	9.3	9.0	16.7	6.8	5.9	ns	**	ns
Shoot length per plant (cm)	75.6	73.2	72.9	153.7	43.4	24.6	ns	**	ns
Mold development	2.30	2.17	1.60	1.43	2.67	1.97	**	**	ns
% cane length dead	22.8	23.3	25.2	13.3	39.9	18.1	ns	**	*
Root growth	3.40	3.07	2.13	3.87	2.30	2.43	**	**	ns
% moisture in canes	56.6	57.1	53.7	57.7	55.9	53.8	**	**	ns

* significant at 5% level
** significant at 1% level
ns no significant difference

After all the data on the tops had been taken, the root wrapping was removed for examination of the roots. It was clear that considerably more root development had taken place in the waxed plants and in those stored at the higher humidities. Since root counting or weighing was impractical, they were evaluated by a ranking system of one to five. One was equal to no new roots, and five was assigned to plants having the heaviest root system, some having as many as 25 new roots up to five inches long. This method of evaluating root development has been found to be valid by Mahlstede and Lana (5). Table 3 shows that the plants at 100 per cent relative humidity produced about 50 per cent more new roots than those stored at 50 per cent relative humidity. The waxed plants also produced about 50 per cent more new roots than the unwaxed.

Moisture percentages in the canes were determined near the end of the experiment on five samples per treatment combination, each from a different plant. The test method was by drying in an oven at 100°C for 24 hours, and results were calculated on a fresh weight basis. Table 3 shows there were highly significant differences both between storage humidities and treatments, although the actual differences in percentage values was relatively small. The canes contained about 3 per cent more moisture when stored at the 100 and 75 per cent relative humidities compared with storage at 50 per cent relative humidity, and the waxed plants contained about 4 per cent more moisture than the unwaxed.

The results of hot water treatment were inconclusive. Water the same temperature as the wax is injurious to the canes as indicated by the fact that the percentage cane length dead for the hot water treated plants was three times that of the waxed plants.

Figure 3 is a graphic summary of the results of this experiment. This figure also indicates the results for individual treatment combinations not shown in Table 3.

Desiccation Experiment

Figure 4 shows the weight loss of the specimens plotted in terms of percentage of original weight against time. The curves for rose show that waxing only the ends of the cane sections did not reduce weight loss appreciably compared with no treatment. This indicates that moisture evaporation was almost as rapid through the sides of the canes as from the cut ends. Waxing the entire cane sections, however, slowed moisture loss considerably, and even after 17 days these specimens did not lose as much weight as the untreated cane sections did in four days.

The curves for althea and privet show that, in contrast with rose, waxing of the cut ends did slow down moisture loss. This indicates that the surface of the stems of these species are inherently better protected from moisture loss.

In the nursery industry it is principally roses that are waxed, and these data indicate one reason why. Roses have less natural protection from desiccation and are therefore more benefited by the waxing process.

SUMMARY

The waxing of the tops of dormant rose bushes to facilitate reestablishment after replanting has been an industry practice for more than twenty-five years, although little experimental data had been available to prove the value of the process. Three experiments were carried out to study the effects of waxing: 1) a field experiment simulating commercial waxing and handling, followed by replanting and observation, 2) a controlled humidity storage experiment, and 3) a laboratory desiccation experiment.

Results of the field experiment showed that waxing increased growth and flower production more than 50 per cent, all measurements considered. The storage experiment showed that waxing increased shoot and root growth considerably while reducing dieback and mold development, although differences in storage humidity had a smaller and not always significant effect. Results of the desiccation experiment showed that waxing of rose canes slowed moisture loss markedly, compared with stems of other woody plants.

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SEASONAL OCCURRENCE OF PYTHIUM GRAMINICOLUM ON ROOTS OF FIELD-GROWN CORN[1]

R.O. Hampton and W.F. Buchholtz

Pythium graminicolum Subr. is a common root pathogen of corn and other graminaceous plants. During the summer of 1956 an effort was made to determine the relative abundance of this fungus on the roots of corn plants of various ages at regular intervals during the growing season.

Ho (3) isolated P. graminicolum readily from the roots of corn growing in the field, but not from the mesocotyl or from the seed. Gerhold (1) isolated only sphaerosporangiate Pythium species from corn seed in early stages of germination in field soil in the laboratory. Ho, Meredith and Melhus (4) recovered P. graminicolum frequently from roots of barley plants in May and June, but not in July. Summers and Buchholtz (5) reported increasing frequency of occurrence of P. graminicolum on the roots of barley growing in the field in late spring and early summer, but P. graminicolum was isolated with greatest frequency from roots of plants 20 days old or older, irrespective of season. With respect to seasonal frequency of occurrence, the data of Haskett (2) tend to confirm those of Summers and Buchholtz.

Procedure

Cultures were made at intervals throughout the season from the roots of corn from plantings at five dates from May 8 to June 6, 1956. The rectangular field plot on which these plants were grown was divided cross-wise into five planting date sub-plots. Planting dates were assigned to sub-plots at random. Five 17-plant rows of an early maturing hybrid, 346, and a late maturing hybrid, 309, were randomly arranged in each planting date sub-plot. Hybrids 346 and 309 had been moderately resistant to Pythium root rot in greenhouse tests.

Eleven series of fungus cultures were completed during the 1956 growing season, the first on May 22, the last on October 9. Each series completed after June 7 consisted of fungus cultures from six root samples taken from the root system of two plants of each of the two hybrid strains from each of the five planting date sub-plots. In the series prior to June 7, fungus cultures were made from 13 root samples from each plant.

A plug of soil was taken so as to contain more or less intact the roots of one plant. The bulk of the soil was carefully removed by hand and

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the remainder gently washed from the roots with a fine spray of water. Roots were kept moist until sections were removed for culturing.

One-fourth-inch sections of several closely associated fibrous roots were clipped from 6 or 12 locations in the root system. The several root sections were cultured individually on coumarin-treated nonnutrient agar in Petri plates. Coumarin had been found to stimulate sporulation of P. graminicolum and at the same time limit growth of contaminating fungi. The percentage of root sections yielding P. graminicolum was recorded for each culture series. The frequency of Fusarium species[2] was recorded at four times during the growing season.

Of the 135 cultures with nematosporangia typical of P. graminicolum, 33 were isolated in pure culture. All produced antheridia of monoclinous origin and plerotic oospores, also typical of P. graminicolum.

Results

Pythium graminicolum was first cultured from corn roots on May 30 (Table 1). The maximum percentage (37.5 per cent) of cultures yielding P. graminicolum during the season was on June 7. The lag to zero percentage in July was associated with scarce precipitation and high daily soil temperature maxima. This relationship is depicted in Figure 1. Total precipitation between June 10 and July 20 was 1.41 inches, which included only three rains of 0.20 inches or more. Only 5 of 120 cultures yielded P. graminicolum on July 7; on July 26, August 2 and August 10 no P. graminicolum was observed in a total of 360 culture plates. P. graminicolum was observed with moderate frequency in cultures made on September 5, September 22 and October 9. As depicted in Figure 1, there had been abundant rainfall in August, and daily soil temperature maxima were down to near 70°F in September.

The percentages of cultures from corn roots in which Fusarium species occurred were as follows: May 22, 75 per cent; May 30, 66.6 per cent; August 2, 57.5 per cent; September 22, 55 per cent.

Pythium graminicolum was not observed in cultures from roots taken from two-week-old plants on May 22. However, it was present in cultures from roots of both two-week-old and three-week-old plants on May 30 (Table 1). Among the cultures made on June 7, a majority of those which contained P. graminicolum were from roots of plants taken from the first (May 8) planting. Roots of plants from all five plantings were available for culturing for the first time on June 22. Although frequency of culturing P. graminicolum was low for all plantings, a majority of cultures which contained P. graminicolum were from roots of plants from the first two plantings.

Conversely, among the cultures made in September and October, a large majority of those containing P. graminicolum were from roots of plants from the last two plantings. P. graminicolum was not cultured from the roots of plants less than 14 days old or more than 132 days old.

[2]The most commonly observed Fusarium species were F. graminearum, F. moniliforme and F. graminum. The usage of Fusarium species in text refers to total of the species observed.

Table 1. Frequency of culturing of *Pythium graminicolum* at intervals during the season from roots of corn planted at five dates.

	Dates of culturing										
	May		June		July		August		September		October
Planting dates	22	30	7	22	7	26	2	10	5	22	9
May 8	0	8	29	5	1	0	0	0	2	0	0
May 16		12	14	8	0	0	0	0	2	0	0
May 23			11	3	1	0	0	0	4	2	0
May 30				2	1	0	0	0	6	4	2
June 6				4	2	0	0	0	5	5	2
Fraction of cultures containing *Pythium graminicolum*	0/48	20/144	54/144	22/120	5/120	0/120	0/120	0/120	19/120	11/120	4/120

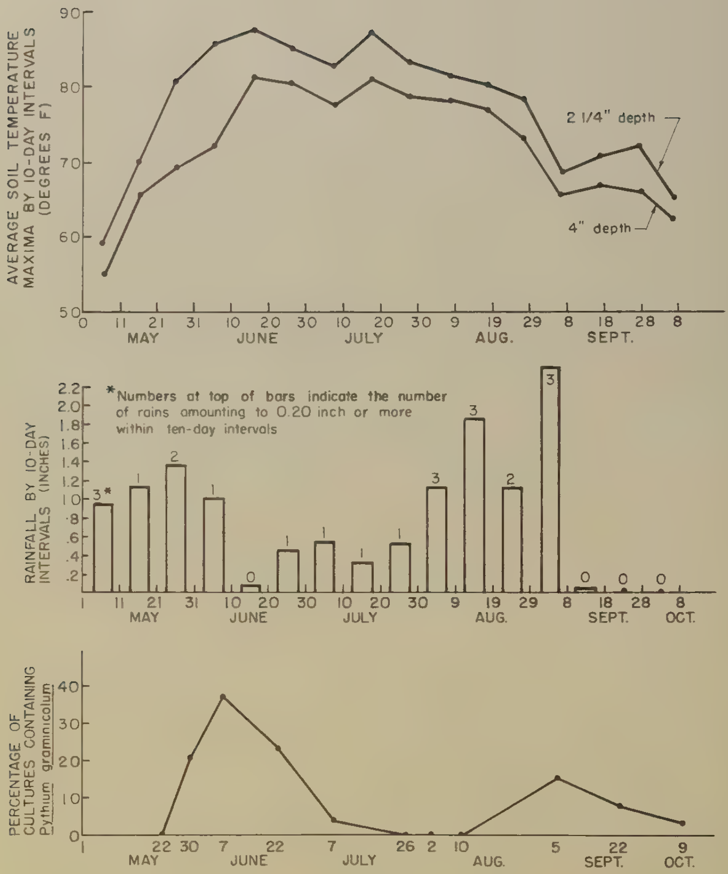

Figure 1. Occurrence of Pythium graminicolum in cultures from corn roots during the 1956 growing season and associated seasonal variations in precipitation and daily maximum soil temperatures.

Table 2. Frequency of culturing Fusarium species, bacteria only, and Pythium graminicolum from crown and lower stalk internodes of field-grown corn.

Location of internode tissue	Date of culturing	Cultures examined	Cultures with Fusarium spp.	Cultures with Bacteria only	Cultures with P. graminicolum
Upper crown	Sept. 5	20[a]	3	17	0
	Sept. 22	20	10	9	0
	Oct. 9	20	13	0	0
Lower crown	Sept. 5	20	12	8	0
	Sept. 22	20	14	3	1
	Oct. 9	20	12	2	2
Lower stalk	Oct. 9	20	18	0	0

[a]The 20 cultures in each category were from one internode from each of two plants of hybrids 309 and 346 from each of five planting dates.

Pythium graminicolum rarely was cultured from old, darkly-lesioned roots. On June 7, among the 54 root sample cultures which yielded P. graminicolum, 47 were from young, finely branched fibrous roots nearly healthy in appearance. Similarly on June 22, 18 of the 22 cultures containing P. graminicolum were from young, nearly white roots.

Pythium graminicolum was cultured somewhat more often from roots of the early-maturing hybrid 346 than from the late-maturing hybrid 309; 75 versus 60, respectively.

On September 5, September 22, and October 9 a total of 140 cultures were made from crown and lower stalk internode tissues. Fusarium species were the predominant fungi in such cultures (Table 2). Furthermore, from September 5 to October 9 there was an increase (3 to 13) in frequency of occurrence of Fusarium species in cultures from upper crown tissues and a decrease (17 to 0) in number of cultures with no fungi (bacteria only). On October 9, 18 of 20 cultures from lower stalk internodes contained Fusarium species and all contained some fungi.

It is pertinent that on September 22 and October 9, Pythium graminicolum was observed in 1 of 20 and 2 of 20 cultures, respectively, from lower crown internodes. One of these, on October 9, was in a culture from tissue taken 20 millimeters above the base of the stem. Other fungi observed in cultures made from lower crown internode tissues on September 22 and October 9 were of Alternaria, Helminthosporium, Curvularia, Penicillium, Rhizopus, sphaerosporangiate Pythium species and Pythium catenulatum.

Discussion

There probably is no adequate measure, under field conditions, of the relative pathogenicity of individual fungus species comprising the root-rot complex of corn in field soils. Frequency of culturing Pythium graminicolum and of Fusarium species from corn roots is not necessarily a measure of the destructiveness of these fungi. It is instead one means by which the variations in destructive potential may be estimated. On this basis, P. graminicolum reached its maximum destructive potential on June 7, on plants 33 days old. Following this date, variations in frequency of occurrence of this fungus in cultures from corn roots was associated positively with variations in precipitation and negatively with variations in average daily soil temperature maxima. These observations are not at variance with those of Summers and Buchholtz (5) for barley, although their last cultures were on July 28 and their July cultures were mostly from roots from May, June and July (late) plantings.

The consistent frequency of culturing Fusarium species (75, 66.6, 57.5 and 55 per cent) at four times during the growing season of 1956 suggested that the occurrence of these fungi in corn roots was not drastically affected by variations in precipitation and soil temperature.

The fact that Pythium graminicolum was isolated predominantly from young, nearly white roots indicates that this fungus is a potential initial incitant in the corn root-rot complex in field soils.

As measured by frequency of occurrence in cultures, Fusarium species were the dominant fungi in tissues of the crown and lower stalk internodes. Although apparent entrance of Fusarium into lower stalk nodes via the leaf sheath was observed during periods of abundant rainfall in August, the somewhat greater frequency of culturing these fungi from the lower than from the upper crown on September 5 and 22 is suggestive of their entrance from infected roots.

The three occurrences of Pythium graminicolum in cultures from lower crown internode tissues of field-grown corn indicate that this fungus may occasionally not be confined to the root system.

Summary

Samples of root segments from corn plants of an early and a late variety planted at five dates from May 8 to June 6, 1956, were placed on nonnutrient agar in Petri plates. High frequency of occurrence of Pythium graminicolum in such cultures was in early June (37.5 per cent) and early September (15.8 per cent). Zero occurrence of P. graminicolum in cultures from root samples taken in late July and early August was associated with scarce precipitation and high daily soil temperature maxima from June 10 to July 20.

P. graminicolum was not cultured from roots of corn less than 14 or more than 132 days after planting. P. graminicolum was cultured predominantly from young, nearly white roots.

Frequencies of occurrence of Fusarium species in cultures from corn roots at four dates were as follows: May 22, 75 per cent; May 30, 66.6 per cent; August 2, 57.5 per cent; September 22, 55 per cent.

Fusarium species were the predominant fungi in cultures from crown and lower stalk internode tissues of corn in September and October. Pythium graminicolum was observed three times in such cultures.

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